

HUGHES MEDAL.

The Hughes Medal is awarded to Sir Joseph Wilson Swan, F.R.S., for his invention of the incandescent electric lamp, and his other inventions and improvements in the practical applications of electricity. Not as directly included in the award, should be mentioned his inventions in dry-plate photography, which have so much increased our powers of experimental investigation.

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*Researches on some of the Physiological Processes of Green Leaves,  
with special Reference to the Interchange of Energy between  
the Leaf and its Surroundings.*

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PART I.—DESCRIPTION OF APPARATUS AND METHODS.

*Introductory.*

In the following series of five papers we have endeavoured to bring together in a connected form the results of various researches carried out in the Jodrell Laboratory at the Royal Gardens, Kew, between the years 1898 and 1901. The present account must be regarded as being supplemented by two previous publications; one on the "Static Diffusion of Gases and Liquids in relation to the Assimilation of Carbon and Translocation in Plants";\* and the other on "The Influence of varying Amounts of Carbon Dioxide in the Air on the Photosynthetic Process of Leaves."†

The main object of the research was, in the first place, to obtain a direct measure of the rate of photosynthesis in a leaf, when it is surrounded by an atmosphere containing an amount of carbon dioxide not far removed from the normal amount of 0.03 per cent.; and secondly to obtain more definite

\* 'Phil. Trans.,' B, vol. 193 (1900), p. 223.

† 'Roy. Soc. Proc.,' vol. 70 (1902), p. 397.

information on the "energetics" of the leaf, especially as regards its power of absorbing and transforming the solar radiation incident upon it.

*Description of Apparatus and Methods.*

In any investigation of the phenomena of assimilation which is based on a direct determination of the rate of intake of the carbon dioxide of ordinary atmospheric air it is evident that, in order to ensure success, the experiments must be carried out on a relatively large scale, both as regards the area of leaf-surface exposed, and the volume of air passed through the apparatus. Another essential condition is that we must have an accurate but not too laborious method for determining the amount of carbon dioxide in the air both before and after contact with the assimilating leaf.

After a considerable amount of preliminary work we adopted the following arrangement of apparatus, which has been used throughout this research, and has proved well adapted to the purpose for which it was devised.

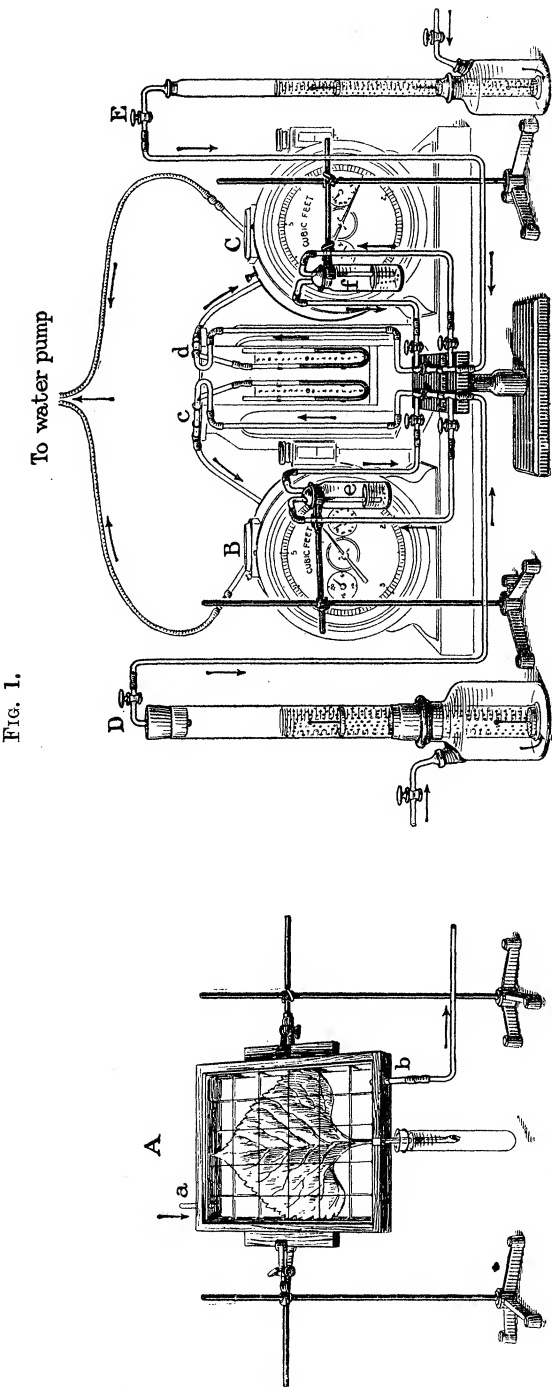
The leaf under experiment is enclosed in a flat rectangular case (A, fig. 1) consisting of a light wooden frame glazed on two sides. The wooden strips before being dove-tailed together to form the frame are carefully dried, and soaked for some time in a bath of hot melted paraffin, in order to render the wood impermeable to air.

The glass plate on one side of the case is permanently fixed, but that of the opposite side is moveable, and drops into a rebate in the frame, into which it may be fixed air-tight with soft wax-mixture after introducing the leaf.\*

In order to maintain the leaf-lamina parallel to the glass sides of the case and to ensure sufficient space for the circulation of the air on both sides, the leaf rests on threads which are laced through small metal eyes screwed into the frame at intervals of about half an inch, and a similar lacing of threads above the leaf serves to fix it in the right position.

If a detached leaf is employed, the petiole passes through an aperture in the side of the case, and dips into a small tube outside, which is filled with water. If, on the other hand, it is desired to experiment on a leaf which is still attached to its plant, there is a slot cut in the wooden frame to about half its depth, into which fits a moveable tongue of wood so arranged that when the leaf is in position the tongue nearly fills up the slot. The spaces around the leaf-stalk and the tongue are made air-tight with the luting mixture already alluded to.

\* The wax luting employed was that recommended by F. F. Blackman, 'Phil. Trans.,' B, vol. 186 (1895), p. 522.



These cases were made in several sizes according to requirements, the largest being capable of taking a fair-sized leaf of the sunflower. An inlet tube *a* for the air is fixed through one side of the frame, and a corresponding outlet *b* on the opposite side, the tubes being respectively above and below the plane of the leaf.

The necessary current of air is drawn through the case by a water-pump, the volume being determined by carefully-standardized meters B and C reading to 20 c.c., and since the volumes of air employed vary from about 200 to 900 litres or more, errors of measurement are practically non-existent.

The air on its way from the leaf-cases to the meters has to pass through the absorption-apparatus D and E presently to be described, and as this introduces a resistance, the air enters the meters at less than atmospheric pressure. This difference of pressure is measured by the mercury manometers *c* and *d* in connection with the inlet to the meters. During an experiment frequent observations are made of these manometers, and also of the barometric pressure and the temperature of the air around the meters, the necessary data for reducing the volumes of air to normal temperature and pressure being thus obtained.

In the glass connection between the absorption-apparatus and the meter there is a small by-pass so arranged with glass taps that a portion of the air-stream can be deflected through small vessels *e* and *f* containing baryta-water.

These act as "guard-tubes," and if the baryta-water remains perfectly clear throughout the experiment, it is an indication that the absorption of carbon dioxide from the air-stream has been complete.\*

The apparatus used for the absorption of the carbon dioxide from the air-stream is similar to the one used by Reiset in his estimations of the carbon dioxide of the atmosphere.†

It is shown in its original form at D in the figure, and consists essentially of a long wide glass tube fixed vertically by means of an india-rubber cap into a wide-mouthed glass vessel furnished with a second opening through which the air enters the apparatus. The height of the tube is always 50 cm., but its width may vary according to the amount of air which has to be passed in a given time.

The lower end of the vertical tube, which is adjusted within a few milli-

\* The absorptive power of the Reiset's apparatus, when due precautions are taken, is so very complete that this portion of the apparatus is almost superfluous.

† 'Compt. Rend.,' vol. 88, p. 1007, and vol. 90, p. 1144; see also Hempel's "Gas Analysis," p. 83.

metres of the bottom of the glass vessel, is closed with a silver plate pierced with fine holes about 0.5 mm. in diameter. There should be not less than ten of these holes per square centimetre.

Two other similar perforated plates are fixed in the vertical tube at heights of about 12 and 25 cm. respectively, and the upper part of the tube is closed with a perforated india-rubber plug, through which passes a tube connecting with the meter. The side-tubulure of the glass vessel is connected either with the leaf-case A or with the outer air as may be required, the liquid for absorbing the carbon dioxide being placed in the glass vessel. When the water-pump is in action the absorbent liquid rises in the vertical tube to a height of about 30 cm., after which air is drawn through the lowest perforated plate and rises through the column of liquid in a rapid stream of small bubbles which are broken up and re-formed at each of the two succeeding plates, thus producing a very effective "scrubbing" action.

The absorption-tubes we have employed are of two sizes, one of them having a diameter of 40 mm. (shown at D of fig. 1) and applicable to rates of flow of from 200 to 400 litres per hour, and another smaller apparatus (shown at E of fig. 1) with a tube diameter of 20 mm. and suitable for volumes of air of from 100 to 150 litres per hour.

This last mentioned apparatus we have had made with glass connections throughout. In this form it is well adapted for the determination of carbon dioxide in the air, and it has the advantage that the whole of the liquid can be used for the final titration instead of an aliquot part as in the case of the larger apparatus.

The apparatus as figured is arranged for the determination of the carbon dioxide of the air, for which the smaller Reiset's apparatus E is used, whilst the larger Reiset D is connected with the current of air coming from the experimental leaf-case. The water-pump is not shown in the illustration.

Instead of baryta, as originally employed by Reiset, we use a 4-per-cent.-solution of pure caustic soda (made from sodium) as the absorbent.

After displacing the air in the absorption-apparatus with air freed from carbon dioxide\* a definite volume of the soda-solution is run into the "Reiset" through the side opening of the large vessel, every precaution being taken to avoid absorption of atmospheric carbon dioxide during the process. The larger apparatus requires 400 c.c. and the smaller 100 c.c. of the solution.

This apparatus acts as a most efficient absorber of the carbon dioxide of ordinary air, and of air artificially enriched with that gas up to ten or

\* The Winkler apparatus is used for this purpose, the air being driven through it with an ordinary india-rubber ball-pump.

twenty times the normal amount. We have made an exhaustive series of test-experiments on this point and have found by introducing a second Reiset apparatus "in series" that there is no falling-off of complete absorption in the first apparatus until from one-fifth to one-fourth of the alkali has been carbonated, and that even when this point is reached the falling-off of absorption is due to a virtual shortening of the column of alkaline solution by the excessive carbonation of its lowest section; for when the contents of the three "stages" of the tube are thoroughly mixed the column once more becomes completely absorbent. In actual practice only a very small fraction of the total amount of caustic alkali is carbonated, and providing the column of liquid is not less than 50 cm. in length the speed of the air-current is practically only limited by the danger attending the ejection of liquid from the tube.

At the completion of an experiment, if the whole amount of alkali has to be submitted to the method of "double titration," which is always the case with the smaller apparatus, the vertical tube is removed from the glass vessel, rinsed out with a little water free from  $\text{CO}_2$ , and over the aperture is slipped an india-rubber cap furnished with a tubulure through which the end of the "acid-burette" can be afterwards passed for titration. In using the larger apparatus it was found more convenient to titrate only an aliquot part of the solution; and here we are met with a practical difficulty which must be referred to somewhat in detail. During the passage through the Reiset's "tower" of large volumes of air only partially saturated with moisture, a certain amount of evaporation necessarily takes place, so that the final volume of the absorbing liquid is somewhat less than the initial volume. In addition to this it is necessary to use a little water to wash the upper part of the "tower," owing to the breaking bubbles of the liquid spurring a little of the solution of soda on to the sides of the tube. The final volume of liquid can be determined from the difference in weight of the apparatus at the beginning and end of the experiment, and the known volume of the original alkaline solution taken. If we represent the original volume of the alkaline solution in cubic centimetres by  $V$ , and the difference between the initial and final weight in grammes of the charged apparatus by  $D$ , then  $V + D$  represents the final volume of the solution in cubic centimetres if no contraction of volume has taken place on adding the wash-water. Theoretically such a contraction undoubtedly takes place, but it cannot appreciably affect the result since it is the special merit of the method of titration employed that an error in the determination of the volumes at any stage of the experiment can only affect the final carbon dioxide estimation in the proportion which this

error of measurement bears to the true volume. In the large Reiset's apparatus we always employed 400 c.c. of the solution of soda, so that if the accumulated errors of measurement amounted to as much as 0.5 c.c., a very unlikely value, the final estimation of the carbon dioxide could only be affected to the extent of  $\frac{0.5 \times 100}{400} = 0.12$  per cent. of the true amount.

When the amount of liquid abstracted from the large apparatus for the final titration is 100 c.c., as is usually the case, the relation which this bears to the original solution is expressed by  $V \sqrt{\frac{100 \times V}{V'}}$ , where V represents the initial, and V' the final volume.

The mode of transferring this 100 c.c. from the Reiset's apparatus to the vessel for titration requires a word of explanation. After rapidly washing down the upper end of the wide tube the plug or stopper is once more inserted, the exit-tube being guarded with a small soda-lime tube. Air, freed from carbon dioxide by passage through a Winkler's absorption-apparatus, is then pumped into the apparatus through one of the tubulures of the lower vessel by means of an india-rubber ball-pump, and the alkaline solution is driven into the wide tube several times in succession until the solution is thoroughly mixed.

After weighing the apparatus a small tube reaching to the bottom of the vessel is inserted into the second tubulure, the upper part of this tube being then connected with a large burette which is filled from below by forcing air down the wide vertical tube. The titration vessel, into which the 100 c.c. of solution is now run from the burette, is a glass cylinder of suitable dimensions furnished with a rubber cap having two apertures through which the ends of the titration-burettes can be passed. In all these operations care is taken that no air can come into contact with the alkaline solution unless it has been previously freed from carbon dioxide by passing through the Winkler's apparatus, and all the open ends of the tubes and burettes are guarded with soda-lime tubes.

#### *The Titration Method.*

Although this has already been described in connection with our work on the static diffusion of gases,\* it is desirable to give a further account of the method in view of its importance in investigations such as we are considering.

There are grave disadvantages connected with any method of carbon

\* 'Phil. Trans.,' B, vol. 193 (1900), p. 289.

dioxide absorption by means of barium hydroxide when the volume of the solution is large and the estimation has to be deduced from the initial and final titration of the liquid. In such a case it is manifest that we have to depend on the determination of *small differences* between two large values, and that the full acid-equivalent of all errors of measurement of the respective solution-volumes will accumulate in the final result, as well as all other errors incident to methods of titration generally. We therefore discarded the barium hydroxide method at an early stage of the enquiry, and turned our attention to one which is free from the cumulative errors to which we have referred. Such a one is found in a method which was originally proposed by P. Hart in 1887,\* for the estimation of the relative amounts of caustic soda and sodium carbonate in soda-ash. As far as we know, this has never been regarded from any other point of view than that of a convenient commercial method, whereas when certain precautions are taken it is capable of a high degree of precision, and really affords one of the most accurate means of determining small quantities of carbon dioxide short of actual measurement of the gas.

It is based on *double titration* with two indicators, one of them phenolphthalëin, sensitive to free carbon dioxide, the other, methyl-orange, only reacting with the excess of mineral acid used in the titration.

If we have a solution of caustic soda which has become partially carbonated, the first stage of the process is the addition of the phenolphthalëin-indicator, followed by a mineral acid (hydrochloric) until the pink colour just disappears. This marks the point of the complete conversion of the neutral into the acid carbonate, or more strictly speaking, the point at which the liberation of the first trace of carbon dioxide takes place. Up to this stage it is unnecessary to take any account of the actual amount of acid used, since this is the starting point for the true titration-process.

Methyl-orange is now added, and this is followed by 1/10 normal hydrochloric acid until the whole of the acid carbonate is decomposed, the volume of the 1/10-normal acid requisite to produce this effect, being of course a measure of the carbon dioxide displaced.

It will be noticed that this method is quite independent of the relations of the total acid-equivalent of the alkali before and after absorption of carbon dioxide, the determination of the carbon dioxide absorbed merely depending on the amount of dilute acid required in each case between the first reaction with phenolphthalëin and the second with methyl-orange. There is also the great advantage that errors in the estimation of the volumes of the solutions

\* 'Journ. Soc. Chem. Ind.,' 1887, p. 347.



will not be accumulated in the result, but will only affect those results in the proportion the errors of measurement bear to the true volume.

Certain precautions are necessary if the highest possible degree of accuracy is required.

In order to avoid an undue increase in the volume of the liquid undergoing titration, which would of course diminish the sensitiveness of the reaction, it is advisable to use in the early stages of the first titration an acid of a strength varying, according to circumstances, between normal and 6-normal, until the pink colour of the phenol-phthalëin becomes somewhat faint: this is followed by 1/10-normal acid to the complete disappearance of the colour. Whilst the stronger acid is being run in it is advisable to keep the solution in constant rotation, otherwise acid carbonate is locally decomposed and carbon dioxide evolved, a misfortune which cannot be rectified.

Caustic soda made from metallic sodium should alone be used, since a trace of alumina or iron interferes with the sharpness of the second titration. A trace of alkaline silicate also interferes with the delicacy of the phenol-phthalëin reaction, a fact which Letts and Blake have also observed,\* but this is not so important a drawback when the above double-titration method is used as it is in methods which are dependent on the exact titration of the whole of the alkali at start and finish.

The actual titrations in our experiments were carried out in cylindrical vessels covered with an india-rubber cap furnished with two tubulures through which the delivery-tubes of the burettes were passed. The use of this cap is unnecessary for the second titration. The burettes used for the soda-solution are filled from stock-bottles through side-tubes, and are furnished at the top with guard-tubes of soda-lime.

In determining the final point in the first titration the meniscus of the liquid is carefully observed, since residual colour can be seen there when it is quite inappreciable in the body of the liquid.

For the second titration a colour-control was always used, containing the same amount of methyl-orange as the liquid titrated, and brought to a constant arbitrary tint of acidity.

When all these precautions are taken the method is sensitive to extremely small differences of carbon dioxide content in the soda-solution employed. In the paper already cited † we have given a series of experiments made with a view to test its limits of delicacy. There is no difficulty in determining in 100 c.c. of an alkaline solution differences in the amounts of carbonate

\* 'Dublin Soc. Proc.,' vol. 9 (1900), p. 152.

† 'Phil. Trans.,' B (1900), p. 291.

corresponding to from 0·1 to 0·15 of a cubic centimetre of carbon dioxide. This corresponds approximately to the carbon dioxide in from 350 to 500 c.c. of air, and since not less than 400 litres of air is passed through the absorption-apparatus for every 100 c.c. of soda-solution, the percentage-error of titration on the amount of carbon dioxide estimated is not more than 0·08 to 0·12 *per cent.* of the true amount.

#### *Determination of the Leaf-Area.*

The most convenient plan for determining leaf-areas with exactness is to place the leaves at the close of an experiment in contact with sensitized paper in an ordinary photographic printing-frame and expose them to light for a short time. The outline of the leaf-print is then followed with an Amsler's planimeter set to read off square centimetres. This is a far more accurate and rapid method than that of cutting out a facsimile of the leaf from paper of a known weight per unit area.

#### *Apparatus for Increasing the Amount of Carbon Dioxide in Air.*

If it is desired to determine the assimilative power of a leaf in an atmosphere artificially enriched with carbon dioxide, we employ a form of apparatus which is a modification of the generator described by Blackman.\* The air-stream before entering the leaf-case is passed through a small tower containing fragments of marble over which is slowly dropped very dilute acid at such a rate as to give approximately the desired amount of carbon dioxide to the air current. Knowing the strength of the acid employed and the volume of air passed, it is easy to adjust the rate of flow of the acid approximately to the desired point.

The stream of air as it leaves this apparatus is divided, one part of the split current passing through the experimental leaf-case, whilst the other passes direct to a Reiset's absorption apparatus and separate meter for the exact estimation of the carbon dioxide it contains.

#### *Rotating Sectors.*

In those cases where it is desired to vary at will, and in a known ratio, the amount of radiant energy falling on a leaf, it is necessary to use some kind of screen which will arrest equal proportions of all the undulations of varying wave-length; in other words the screen must exercise no "selective absorption" on the radiations.

\* 'Phil. Trans.,' vol. 186 (1895), p. 495.

The most satisfactory way of meeting this difficulty is to employ the method of *rotating sectors* which has been largely used by Abney in his investigations on colour-measurement. For this purpose the Cambridge Scientific Instrument Company constructed for us an apparatus consisting of a series of moveable metal sectors, which could be adjusted on a revolving axis in such a manner as to cut off from an object placed under the sectors any desired amount of the total solar radiation falling on it.

The motive power was, in our case, supplied by a small water turbine, but the use of a small electric motor would much simplify the construction. The broken disc, formed by the sectors, could be inclined at any desired angle, and when rotated in front of a leaf, placed parallel to it, cut off a perfectly definite proportion of the solar radiation, and the effect could be compared with that produced by the full radiation falling on another leaf alongside the first.

*Measurement of the Intensity of Radiation.*

The intensity of radiation falling on the leaf-surface was determined by means of a Callendar's radiometer, consisting of a pair of differential platinum thermometers, the one black and the other bright, wound on flat plates of mica and placed side by side in a flat rectangular glazed case, which was mounted on an adjustable stand so that the radiometer could be placed alongside the leaf and in exactly the same plane.

The platinum coils occupy an area of about 75 sq. cm., and the difference in temperature between them, which is proportional to the intensity of the vertical component of the radiation, is determined by connecting them with a Callendar's recorder, consisting essentially of a "Wheatstone's bridge or potentiometer in which the movement of the slider along the bridge-wire is automatically effected by relays, worked by the current passing through the galvanometer between the bridge-arms."\*

A simple form of planimeter attached to the instrument integrates the curve drawn by the pen on the revolving drum, and from the known constants of the instrument the planimeter-readings can be readily converted into water-gramme-units (calories) per square centimetre per minute, due regard being paid to any extra resistances which it may be necessary to insert during the course of the experiment for the purpose of keeping the pen within the range of the drum.

We are much indebted to Professor Callendar for his assistance and advice

\* Professor Callendar described his recorder in detail in 'Engineering' for May 26, 1899. For a general description of the Callendar's radiometer, see 'British Association Report' for 1898, p. 796.

in carrying out the preliminary work connected with this instrument, and especially for the labour he bestowed on the calibration of the radiometer in absolute thermal units.

The radiometer and recorder were constructed by the Cambridge Scientific Instrument Company, and their cost was defrayed by the Government Grant Committee of the Royal Society who kindly put the instruments at our disposal for this research.

When a bridge-wire No.  $\frac{1}{2}$  is used in the recorder of this particular instrument, 100 scale-divisions = 1 ohm, and with the radiometer in sunshine in the horizontal position, 1 scale-division (= 4 mm.) is equivalent to a radiation of 0.0070 calorie per sq. cm. per minute. With the radiometer in bright sunshine and inclined at an angle of  $45^\circ$  to the horizon, 1 scale-division = 0.0074 calorie per sq. cm. per minute, the difference in this case being due to the influence of air-convection on the coils.

## PART II.—EXPERIMENTS ON ASSIMILATION AND RESPIRATION.

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Section (1).—*The Rate of Assimilation of Leaves as deduced from the Direct Estimation of the Carbon Dioxide absorbed in the Photosynthetic Process.*

In a previous paper dealing with the influence of varying amounts of carbon dioxide on the photosynthetic process of leaves,\* it was shown that, providing there is an excess of radiant energy of the right quality incident on the leaf, *the rate at which photosynthesis takes place is approximately proportional to the mean partial pressure of the carbon dioxide in the air supplied to the leaf during the experiment.*

Another way of expressing this fact is as follows; If we denote the partial pressure of the carbon dioxide of ordinary air by  $p$ , that of artificially-enriched

\* 'Roy. Soc. Proc.,' vol. 70 (1902), p. 397.

air by  $p'$ , the rate of assimilation in ordinary air by  $a$ , and that in enriched air by  $a'$ ; then, within certain limits,  $p/a = p'/a'$ .

Our experiments have shown that this relation of partial pressure to assimilation certainly holds good up to 15 parts of carbon dioxide per 10,000 of air, that is to say, up to a concentration of five times the normal amount; but it is highly probable that this by no means expresses the upward limit of the application of this rule, which is one of considerable practical importance when we desire to determine the true rate of assimilation in ordinary air, as will be seen from the following considerations.

The actual amount of carbon dioxide which has been abstracted from a measured volume of air passed over the leaf is expressed by the difference in the amount of carbon dioxide in the air on entering and emerging from the leaf-case, and since the mean carbon dioxide-content of the air in contact with the leaf must necessarily be less than that of the outer air, a correction must be made if we desire to ascertain the true rate at which the leaf would assimilate under free-air conditions, all other conditions being constant. The above rule enables us to make such a correction, the magnitude of which will be readily seen from the following concrete example taken from an actual experiment.

A leaf of *Catalpa bignonoides* having an area of 157·45 sq. cm. was enclosed in its glazed case and submitted to intermittent sunshine for six hours, during which time 322·57 litres of air were passed over it. From an analysis of the ingoing and outgoing air it was found that the leaf had abstracted 32·58 c.c. of carbon dioxide (at 0° and 760 mm.), which is equivalent to an assimilation of 3·448 c.c. per square decimetre per hour. Since, however, the outer air as it entered the leaf-case contained 2·80 volumes of carbon dioxide per 10,000 volumes of air, whilst the emerging air contained only 1·79 volumes, the mean carbon dioxide-content of the air in contact with the leaf was only  $\frac{2\cdot80 + 1\cdot79}{2} = 2\cdot295$  per 10,000. Hence, from the above rule of partial pressures, the amount of carbon dioxide which the leaf would have assimilated in the outer air, all other conditions being the same, is  $\frac{3\cdot448 \times 2\cdot8}{2\cdot295} = 4\cdot206$  c.c. of carbon dioxide per square decimetre per hour.

The correction in this case, therefore, which is a somewhat extreme one, is +22 per cent.

Although such a method as we are considering ought to give, with a fair approximation to accuracy, a measure of the *effective assimilation* going on in the leaf, the results are subject to a further correction if we desire to know the exact amount of photosynthetic work accomplished, since there is active

respiration going on in the leaf-cells, and the carbon dioxide due to this process is not evolved, but undergoes re-elaboration under the influence of the light. The intensity of the respiratory function increases, within certain limits, with the temperature. Under the conditions of the particular experiment just cited the re-synthesised carbon dioxide of respiration amounted to about 0.5 c.c. per square decimetre per hour, so that the total photosynthetic work accomplished is represented by  $4.206 + 0.5 = 4.706$  c.c. of carbon dioxide per square decimetre per hour, being a further increase of about 11 per cent.

In experiments where it is only required to know the *effective assimilation*, that is to say, that portion of the process which can alone contribute to an actual increase in weight of formative carbohydrate in the plant, this correction need not be applied.

We may now consider the results of a series of experiments carried out on the lines indicated, and for the purpose of determining the rate of the effective assimilation of leaves in air containing the normal amount of carbon dioxide.

The volumes of air and carbon dioxide are reduced to normal temperature and pressure (N.T.P.) and the carbon dioxide which has been fixed by the leaf is corrected to the partial pressure of that gas existing in the outer air at the time of the experiment.

The comparatively large scale on which these experiments have been carried out is perhaps best realised by reference to Columns (3) and (6) in the following table, which give respectively the area of the leaf employed and the number of cubic centimetres of carbon dioxide absorbed and utilised by the leaf during the full time that the experiment lasted, amounting in some cases to upwards of 140 c.c. of the gas.

Column (7) gives the volume of carbon dioxide (measured at normal temperature and pressure) which would have been assimilated by 1 square decimetre of leaf per hour, under a partial pressure equivalent to that of the  $\text{CO}_2$  in the outer air at the time, and from this value we can readily deduce the actual weight of carbohydrate synthesised for unit-area and unit-time, provided we know the mean empirical formula of the carbohydrate.

If the carbohydrate is a hexose (*e.g.*, *glucose* or *fructose*) or one with the general formula  $\text{C}_n\text{H}_{2n}\text{O}_n$ , then the absorption by the leaf of one part by weight of carbon dioxide corresponds to the synthesis of 0.681 parts of the carbohydrate. If, on the other hand, we assume that it is *cane-sugar* which is synthesised, or any sugar of the  $\text{C}_{12}\text{H}_{22}\text{O}_{11}$  class, then the disappearance of one part by weight of carbon dioxide corresponds to the synthesis of 0.647 parts of the body in question.

Finally, if we assume that *starch* or *inulin* is the synthesised product, having the formula  $C_6H_{10}O_5$ , then one part by weight of carbon dioxide can give rise to 0.613 parts of the carbohydrate.

In considering which factor we ought to take for calculating the increase in dry weight of the leaf from the amount of carbon dioxide fixed, we must bear in mind that the question is quite independent of the nature of the primary product of assimilation, and turns on the relative proportion of the above three classes of carbohydrates at the close of the experiment.

In two separate determinations of the starch and sugars of leaves of *Tropæolum majus* in full assimilation, Brown and Morris found\* them apportioned as follows, the determinations being expressed as percentages on the dry weight of the leaves.

	I.	II.
Starch .....	3.693	5.425
Cane-sugar .....	9.980	7.330
Dextrose .....	0.000	0.000
Lævulose.....	1.410	2.110
Maltose .....	2.250	2.710
Total per cent. ...	17.333	17.575

By multiplying each one of these values by the factor appropriate to the particular class of carbohydrate as stated above, we obtain average values as follows:—

Factor deduced from I .....	0.642
„ „ II .....	0.640

These are not far removed from the arithmetical mean of the three values for the three different classes of carbohydrates, which is 0.646.

The “carbohydrate-factor” we have used for converting carbon dioxide assimilated into its equivalent by carbohydrate is 0.640.

Since 1 c.c. of carbon dioxide at normal temperature and pressure weighs 0.00196, the number of c.c. given in Column (7), Table I, multiplied by (0.00196  $\times$  0.640) should give *the corresponding weight of carbohydrate produced in one square decimetre of leaf per hour*. These values are shown in the last column of Table I.

Before drawing any conclusions from the above results as to the rate of assimilation in ordinary air of the usual carbon dioxide-content, we will give the details of a further set of experiments in which the air supplied to the leaf-cases had been previously enriched with a further determinate amount of that gas.

\* ‘Journ. Chem. Soc.,’ 1893, Trans., p. 671.

Table I.—Assimilation in Ordinary Air.

(1) Description of leaf and general conditions.	(2) Temperature C.	(3) Area of leaf in square centimetres.	(4) CO <sub>2</sub> in air, parts per 10,000.		(5) Duration of experiment in hours.	(6) CO <sub>2</sub> absorbed during experiment in cubic centimetres, N.T.P.	(7) CO <sub>2</sub> assimilated per square decimetre of leaf per hour in cubic centimetres.	(8) Carbohydrate assimilated per square decimetre per hour in grammes.
			CO <sub>2</sub> in air, parts per 10,000.	Mean CO <sub>2</sub> of air in leaf case.				
(1) <i>Helianthus annuus</i> . 25/8/98. Attached to plant. Strong diffused light of northerly sky ...	21°·1	743·1	2·22	2·80	2·0	36·89	3·126	0·00392
(2) <i>Helianthus annuus</i> . 29/8/98. A detached leaf. Diffused light of northern sky .....	19°·0	743·1	1·92	2·80	6·41	143·68	4·399	0·00551
(3) <i>Helianthus annuus</i> . 25/8/98. A detached leaf. Strong diffused light, under thin canvas screen.....	21°·1	312·1	2·33	2·80	4·0	29·97	2·885	0·00361
(4) <i>Helianthus annuus</i> . 25/8/99. Detached leaf. Strong diffused light under canvas screen	26°·8	336·4	2·25	2·80	4·0	41·67	3·853	0·00483
(5) <i>Helianthus annuus</i> . 29/8/99. Detached leaf. Day cloudy, but strong diffused light.....	19°·4	275·9	2·29	2·80	3·25	29·37	4·005	0·00502



(6) <i>Helianthus annuus</i> . 7/8/00. Leaf still attached to plant. Intermittent sunshine. No screen .....	22°·1	760·1	2·02	2·71	4·9	79·50	2·863	0·00359
(7) <i>Helianthus annuus</i> . 11/8/00. Leaf still attached to plant. Bright sunshine. No screen.....	47°·1	881·2	2·72	2·79	3·7	6·98	0·219	0·00027
N.B.—The temperature of the leaf-case was very high, but the leaf still remained turgid. It will, however, be noted that effective assimilation was almost in abeyance, owing to the high temperature.								
(8) <i>Helianthus annuus</i> . 17/8/00. Leaf still attached to plant. Sunshine. No screen used	41°·8	979·6	2·93	2·82	4·2	nil	nil	nil
N.B.—Owing to the high temperature effective assimilation was entirely in abeyance, respiration being predominant, as shown by emergent air containing more CO <sub>2</sub> than entering air.								
(9) <i>Tropaeolum majus</i> . 4/9/00. A detached leaf. Diffused sunlight through canvas screen....	21°·7	130·1	2·705	2·86	3·3	6·43	1·593	0·00198
(10) <i>Tropaeolum majus</i> . 7/9/00. Detached leaf. Sunshine. Case under canvas .....	25°·9	193·5	2·345	2·75	5·0	20·11	2·437	0·00805
(11) <i>Tropaeolum majus</i> . 11/9/00. Conditions same as last ...	24°·9	204·0	2·57	2·80	4·85	12·03	1·324	0·00166
(12) <i>Tropaeolum majus</i> . Conditions same as last .....	24°·2	169·7	2·725	3·00	4·9	14·57	1·929	0·00241

Table I.—Assimilation in Ordinary Air—*continued*.

(1) Description of leaf and general conditions.	(2) Temperature C.	(3) Area of leaf in square centimetres.	(4) CO <sub>2</sub> in air, parts per 10,000.		(5) Duration of experiment in hours.	(6) CO <sub>2</sub> absorbed during experiment in cubic centimetres, N.T.P.	(7) CO <sub>2</sub> assimilated per square decimetre of leaf per hour in cubic centimetres.	(8) Carbohydrate assimilated per square decimetre per hour in grammes.
			CO <sub>2</sub> in air, parts per 10,000.	Mean CO <sub>2</sub> of air in leaf case.				
(13) <i>Tropaeolum majus</i> . Detached leaf. Strong diffused light through canvas screen .....	20°·6	134·2	2·665	2·91	5·3	12·56	1·928	0·00241
(14) <i>Tropaeolum majus</i> . Two detached leaves, A and B, ex- posed simultaneously. Sunshine. Under canvas screen — Leaf A .....	22°·0	130·3	2·70	2·85	5·0	8·66	1·403	0·00176
Leaf B .....	21°·8	137·1	2·66	2·85	5·0	11·07	1·730	0·00217
(15) <i>Catalpa purpurea</i> . 26/7/98. A detached leaf, exposed to intermittent sunshine.....	22°·7	304·21	2·415	2·92	4·5	26·22	2·315	0·00290
(16) <i>Catalpa bignonioides</i> . 31/8/99. Detached leaf. Inter- mittent sunshine .....	20°·0	417·6	2·05	2·80	4·0	45·65	3·782	0·00468
(17) <i>Petasites albus</i> . 6/6/00. Detached leaf under canvas screen in sunlight .....	19°·8	285·9	2·52	2·82	3·2	23·46	2·869	0·00359

(18) <i>Petasites albus</i> . 26/6/00. Detached leaf. Intermit- tent sunshine .....	17°·0	295·0	2·56	2·84	5·3	29·38	2·084	0·00261
(19) <i>Petasites albus</i> . 5/7/00. Detached leaf. Inter- mittent sunshine. Screen used part of time .....	25°·2	256·1	2·59	2·86	5·3	34·035	2·769	0·00347
(20) <i>Polygonum Weyrichii</i> . 19/6/00. Detached leaf .....	21°·0	305·2	2·24	2·82	5·0	57·36	4·782	0·00593
(21) <i>Polygonum Weyrichii</i> . 22/6/00. Detached leaf. Canvas screen in sunshine .....	19°·3	378·6	2·38	2·84	4·2	48·66	3·651	0·00458
(22) <i>Polygonum Weyrichii</i> . 3/7/00. Detached leaf under canvas screen in intermittent sunlight ...	28°·3	415·1	2·40	2·93	5·1	48·08	2·772	0·00347
(23) <i>Polygonum Weyrichii</i> . 11/7/00. Detached leaf under canvas screen in bright sunshine. Very hot day .....	37°·9	384·1	2·61	2·84	4·95	28·12	1·609	0·00201

N.B.—Effective assimilation has been reduced in this experiment by high temperature.

Table II.—Assimilation in Air containing more than the Normal Amount of Carbon Dioxide.

Description of leaf and general conditions.	(1) Temperature, C.	(2) Area of leaf in square centimetres.	(3) Mean CO <sub>2</sub> content of air in contact with leaf. Parts per 10,000.	(4) Duration of experiment in hours.	(5) CO <sub>2</sub> absorbed during experiment in cubic centimetres at N.T.P.	(6) CO <sub>2</sub> assim- ilated per square deci- metre per hour in cubic centimetres.	(7) Carbohydrate assimilated per square decimetre per hour in grammes.
(1) <i>Helianthus annuus</i> . 18/8/98. Leaf still attached to plant. Continuous sunshine .....	27°·0	617·5	16·41	4·41	622·9	22·87	0·02869
(2) <i>Helianthus annuus</i> . 23/8/98. Facing bright northerly sky. Leaf attached to plant .....	23°·7	863·7	14·82	2·75	428·2	18·02	0·02261
(3) <i>Helianthus annuus</i> . 23/8/99. Intermittent sunshine. Leaf detached ..... (Carried on simultaneously with (3) of Table I)	22°·6	303·9	10·4	4·0	218·9	18·00	0·02257
(4) <i>Helianthus annuus</i> . 25/8/99. In sunshine under canvas screen (Carried on simultaneously with (4) of Table I)	28°·2	312·7	9·95	4·0	205·1	16·39	0·02056
(5) <i>Helianthus annuus</i> . 29/8/99. Detached leaf. Cloudy day..... (Carried on simultaneously with (5) of Table I)	19°·3	411·2	16·4	3·25	243·2	18·15	0·02277
(6) <i>Catalpa bignonioides</i> . Detached leaf. Weather cloudy ..... (Carried on simultaneously with (16) of Table I)	20°·0	433·6	12·65	4·0	172·5	9·94	0·01247

The rate of assimilation of leaves in air which has been artificially enriched with carbon dioxide is seen to be considerably greater than it is in normal air. In a previous communication direct proof has been given \* that up to five or six times the normal amount of  $\text{CO}_2$ , assimilation, *cæteris paribus*, is approximately proportional to the amount of that gas present. A further general proof of this proposition may be obtained by reducing the values given in the last column of Table II in the proportion of the amounts of carbon dioxide in the leaf-cases (as given by Column (3)) to that of average air of from 2·8 to 3 parts per 10,000. A series of values is then obtained of the same order of magnitude as those of the last column of Table I.

Section (2).—*A Comparison of the Direct Method of Determining the Rate of Assimilation in Ordinary Air with the Weighing Method of Sachs.*

Up to about twenty years ago the only known methods for determining the rate of assimilation under free air conditions were based on an estimate, more or less exact, of the increase in dry weight of a plant during a considerable period of its growth. In 1884, Sachs, in his classical paper "Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter," † asserted that with due precautions the varying dry weights of known areas of leaf-lamina could be used as measures of the amount of carbohydrate produced in the leaf.

In the case of a detached leaf of *Helianthus annuus*, he found that there was an increase in weight during several hours of favourable isolation corresponding to 0·01648 gramme per square decimetre of leaf area per hour. Under similar conditions detached leaves gained more in weight than leaves still attached to the plant, a result which Sachs attributed to the simultaneous depletion of the leaf in the latter instance, owing to the migration of some of the products of assimilation into the stem of the plant. By adding the rate of *loss* during the hours of darkness to the rate of *gain* during insolation, Sachs obtained certain values which he believed to represent approximately the rate of assimilation during the day time. For *Helianthus* and *Cucurbita* his final results are given below. For purposes of comparison with our own results we have calculated the corresponding amounts of carbon dioxide equivalent to the carbohydrate which this increase is supposed to indicate.

\* 'Roy. Soc. Proc.,' vol. 70, p. 399.

† 'Arbeit. d. Bot. Institut. Würzburg,' vol. 3, p. 23.

Table III.—Total Assimilation per Square Decimetre of Leaf per Hour, according to Sachs.

	Grammes increase per square decimetre per hour.	Equivalent of CO <sub>2</sub> in cubic centimetres.
<i>Helianthus annuus</i> .....	0·01882	15·00
<i>Cucurbita Pepo</i> .....	0·01502	11·97

In repeating these experiments in 1892, Brown and Morris\* obtained the following results by the Sachs method, in which no correction is made for the assumed simultaneous depletion in the case of the leaves still attached to the plant.

Table IV.

	Grammes increase per square decimetre per hour.	Equivalent of CO <sub>2</sub> in cubic centimetres.
Expt. I. <i>Helianthus annuus</i> —		
A. Detached leaf .....	0·00985	7·85
B. Still attached to plant..	0·00460	3·66
Expt. II. <i>Helianthus annuus</i> —		
A. Detached leaf .....	0·0100	7·97
B. Still attached to plant..	0·0071	5·66

When we compare the results of Table I obtained for *Helianthus* by direct determination of the carbon dioxide taken in by the leaf with those deduced by Sachs from his weighing method, we find a very great discrepancy, the apparent rate of assimilation in the former case being only one-third to one-fifth of what it is in the latter. On the other hand, in the experiments of Brown and Morris, where diurnal depletion of the leaf is not assumed, the discrepancy is less, but even here, in the case of the detached leaves, the weighing method has given an apparent rate of assimilation about double that of the direct method by CO<sub>2</sub> measurement.

In considering the probable cause of these discrepancies we must first

\* 'Journ. Chem. Soc.,' 1893, Trans., p. 625.

discuss how far Sachs was justified in adding the hourly *gain* of weight of the leaf during the day to the hourly *loss* during the night in order to arrive at his result. He was led to this correction by observing that in placing two leaves under similar external conditions, but having one detached with its petiole in water, whilst the other was still attached to the plant, the gain in weight of the detached leaf per unit area was greater than that of the attached leaf. Whilst, for instance, the detached leaf gained in weight at the rate of 0·01648 gramme per decimetre per hour, the leaf on the plant only gained at the rate of 0·00914 for the same area and time, thus showing a falling-off of 44·5 per cent.

The experiments of Brown and Morris also showed the same falling off in weight-increase in the case of the attached as compared with the detached leaves as shown in Table IV, this falling-off being 53 per cent. in Experiment (1) and 30 per cent. in Experiment (2), or an average of 41·5 per cent., *i.e.*, almost exactly Sachs' value.

There can be no doubt about the different behaviour of attached and detached leaves under the above conditions, but we believe the fact has received an erroneous explanation which has led to a considerable over-estimate of the rate of assimilation as deduced from the Sachs weighing method.

When the rate of assimilation of two similar leaves placed side by side is determined by the actual amount of carbon dioxide taken into the leaf, we have found that, contrary to what might have been expected, the leaf attached to the plant assimilates at a *less* rate than the detached leaf with its petiole in water. This is shown by the two experiments following, exactly similar leaves being enclosed in similar leaf-cases and exposed under identical conditions of insolation and air-current.

The falling-off in the assimilation of the attached leaf as compared with the detached leaf is 34·3 per cent. in Experiment (1) and 54·8 per cent. in Experiment (2), the mean being 44·5 per cent., which corresponds almost exactly with the differences in weight of the attached and detached leaves of *Helianthus* in the previously-recorded experiments of Sachs. But in this instance we cannot fall back upon leaf depletion of the attached leaf as the explanation, since our method, unlike that of Sachs' is quite independent of any migration of the products of assimilation during the experiment, for it is based on the actual intake of carbon dioxide into the leaf. We are forced to conclude therefore that the differences recorded in Table V are due to *differences in the stomatal openings* in the two cases, the stomata of the detached leaves being more widely opened than those of the leaf still attached to the plant.

Table V.—Relative Rate of Assimilation of *attached* and *detached* Leaves of *Catalpa bignonioides*, determined by Estimation of CO<sub>2</sub> absorbed from ordinary Air.

Plant.	Tempera- ture, C.	Area of leaf in square centimetres.	CO <sub>2</sub> in air, parts per 10,000.		Duration of experi- ment in hours.	CO <sub>2</sub> absorbed during experiment in cubic centimetres, N.T.P.	CO <sub>2</sub> assimilated per square decimetre of leaf per hour.	Carbo- hydrate assimilated per square decimetre per hour, in grammes.
			Mean CO <sub>2</sub> of air in leaf-case.	CO <sub>2</sub> in outer air.				
(1) <i>Catalpa bignonioides</i> .								
8/8/99. A. Detached leaf ...	—	284.9	2.268	2.80	5.00	35.23	3.053	0.00382
B. Attached leaf ...		384.2	2.295	2.80	5.00	31.56	2.003	0.00251
(2) <i>Catalpa bignonioides</i> .								
15/8/99. A. Detached leaf ...		446.9	2.496	2.80	4.33	29.96	1.735	0.00217
B. Attached leaf ...		463.4	2.660	2.80	4.33	14.95	0.784	0.00098



From the physical considerations adduced in a previous paper it has been shown that gaseous diffusion through stomata must vary, other things being equal, with the linear dimensions of the openings, and it appears to be a fair deduction that the linear dimensions of the stomata in a leaf still attached to the plant are about 45 per cent. less than those of the stomata of the same leaf after separation from the plant and immersion of the petiole in water.

That the artificial conditions under which such a detached leaf is placed should have an influence on the delicate self-regulating mechanism of the guard-cells of the stomata is perhaps scarcely to be wondered at, especially when we bear in mind that a leaf which is still attached to its plant is receiving water more or less highly charged with salts derived from the soil, which must exert a distinct osmotic effect on the leaf-cells, whereas only pure water is supplied to the cut leaf.

Whether or not this is the true explanation of the observed differences the fact remains that for equal areas, and under similar conditions, the rate of assimilation of a leaf still attached to the plant is about 45 per cent. less than that of a detached leaf, and this must in future be taken into consideration in interpreting the experiments of Sachs, in which equality in assimilatory power in the attached and detached leaves has hitherto been assumed.

It would appear therefore that Sachs was not justified in making the correction for diurnal depletion which he did; but even if we neglect this supposed depletion and assume that none of the products migrate from the leaf to the stem during the insolation, the apparent increase in weight of an attached leaf, both in the experiments of Sachs and those of Brown and Morris, still indicates a rate of assimilation about twice that indicated by the direct measurement of the intake of carbon dioxide, as given in Table I.

The first explanation of the discrepancy which suggests itself is that the conditions for assimilation in our leaf-cases are not so favourable as those which exist when the leaf is freely exposed to the air. We have already seen that when cut leaves are employed the advantage in one respect (provisionally ascribed to the wider opening of the stomata) is in the direction of obtaining more rapid photosynthesis than in leaves attached to the plant. There is another aspect of the subject, however, which requires careful consideration. Owing to the practical difficulty of keeping down the temperature of the leaf enclosed in its case it is impossible to carry out such experiments successfully in full sunshine, and they must be made either on cloudy days, or by moderating the sunshine by an artificial "cloud" in the nature of a thin canvas screen. Unless it can be

shown that in this moderated illumination the particular rays active in the photosynthetic process are still considerably in excess of the requirements of the chloroplasts for the particular partial pressure of the carbon dioxide employed, there will be room for doubting whether in this respect the leaf enclosed in its case is not at a disadvantage as compared with a leaf receiving the full solar radiation under free-air conditions.

We have made numerous experiments in two different directions in order to throw some light on this point. In the first place we find that under this moderated illumination, whether the diminution of intensity is due to natural cloud or to the interposition of a thin canvas screen, the assimilatory process always readily responds to slight increases in the amount of the carbon dioxide in the air of the case, and that within certain limits fixation of carbon dioxide is proportional, or nearly so, to the partial pressure of that gas. This fact in itself indicates that the special rays active in photosynthesis are still present in the moderated illumination in excess of the requirements of the leaf when it is in air of normal CO<sub>2</sub> content.

Another, and still more conclusive mode of experiment was to place two similar leaves in their cases under the thin canvas screen, cutting off a certain determinate amount of the light from one of them by means of the apparatus with revolving sectors, already described in Part I, and measuring the relative rate of assimilation by estimating the carbon dioxide absorbed from a stream of ordinary air passed through the cases.

The results of such a series of experiments are recorded in the following Table VI. It will be seen that the sunlight passing through the light canvas screen, which absorbed about two-thirds of the solar radiation, had to be further reduced by the radial sectors to *one-quarter* of its intensity before there was any sensible effect in reducing the rate of assimilation; thus showing that the light which passed through the screen still contained more of the particular grade of radiant energy active in photosynthesis than the chloroplasts of the leaf could utilise. This appears to us to be a strong argument in favour of the leaves enclosed in the cases being under no disadvantage as compared with those under free-air conditions. In fact, for reasons already given, it would appear that we might expect better results from the *cut* leaves when placed under these artificial conditions than are attainable with leaves still attached to the plant in the open.

Table VI.—Influence of Reduced Illumination of Leaves of *Tropaeolum majus* on Rate of Assimilation. Ordinary air used.

- A. Leaves exposed to sunlight which had passed through thin canvas screen.  
 B. Leaves also under canvas screen, but light still further reduced by revolving sectors.

N.B.—The volumes of carbon dioxide absorbed by the leaves are corrected to the partial pressure of that gas in outer air.

	Tempera- ture in leaf- case.	CO <sub>2</sub> assimilated by leaf per decimetre per hour in cubic centimetres (corrected).	Carbo- hydrate correspond- ing to CO <sub>2</sub> in grammes.
Experiment (1).— 4/9/00. A. Full illumination (under screen) .....	21°·7	1·692	0·00212
B. Half illumination (under screen) .....	20°·3	2·029	0·00254
Experiment (2).— 18/9/00. A. Full illumination (under screen) .....	20°·6	1·919	0·00240
B. Half illumination (under screen) .....	19°·6	2·047	0·00256
Experiment (3).— 13/9/00. A. Full illumination (under screen) .....	24°·2	1·926	0·00241
B. Quarter illumination (under screen) .....	22°·2	1·311	0·00164

The following Table VII gives the results of a further series of experiments in which the rate of assimilation of detached leaves under free-air conditions was deduced from the ordinary half-leaf weighing method of Sachs, species of plants being taken in which the leaf-symmetry is especially well marked. The individual leaves were selected with great care to ensure as close a correspondence as possible between the two halves.

Table VII.—Rate of Assimilation deduced from Half-leaf weighing Method.

Species of plant.	Time of insolation in hours.	Area in square centimetres.	Dry weight in grammes.	Increase in dry weight per square decimetre per hour, in grammes.
(1) 3/8/98.— <i>Catalpa bignonioides</i> —				
A. Before insolation.....	—	259·1	1·1188	—
B. After insolation .....	7·0	276·8	1·3488	0·00791
(2) 9/8/98.— <i>Catalpa bignonioides</i> —				
A. Before insolation.....	—	225·6	0·9729	—
B. After insolation .....	5·0	194·1	0·9740	0·01370
(3) 16/8/98.— <i>Catalpa bignonioides</i> —				
A. Before insolation.....	—	418·35	1·8546	—
B. After insolation .....	3·25	438·45	2·1812	0·01660
(4) 2/6/98.— <i>Sparmannia africana</i> —				
A. Before insolation.....	—	150·0	0·6303	—
B. After insolation .....	6·25	150·0	0·6636	0·00387
(5) 3/6/98.— <i>Sparmannia africana</i> —				
A. Before insolation.....	—	125·0	0·5086	—
B. After insolation .....	6·0	125·0	0·5287	0·00268
(6) 22/6/98.— <i>Sparmannia africana</i> —				
A. Before insolation.....	—	125·0	0·4295	—
B. After insolation .....	6·5	125·0	0·4734	0·00540

N.B.—In Experiments (4), (5), and (6) equal areas were cut from the two halves of the leaves before and after insolation. In the other experiments the entire half leaves were taken.

In the results recorded up to this point we have seen that the general tendency of the Sachs' weighing method is to give a much higher estimate of the rate of assimilation of leaves in ordinary air than is given by a method based on the measurement of the actual intake of carbon dioxide. The justice

of this comparison of methods rests so far on the assumption that the leaves enclosed in their cases are under conditions which, at any rate, are not *less* favourable to assimilation than those experienced by leaves assimilating in free air. The reasons in favour of the correctness of this assumption have been already given, but in order to meet any possible objections on this point we instituted another series of experiments *in which the increase in dry weight and the simultaneous intake of carbon dioxide could be determined on the same leaves.*

These experiments were made on leaves of *Catalpa bignonioides* in the following manner. Four selected symmetrical leaves, whilst still attached to the plant, were covered with tin-foil in the evening in order to ensure their effective depletion by the morning of the following day. These leaves were then carefully detached by cutting through the petioles under water, and were brought into the laboratory. From each pair of leaves the alternate right and left halves were then cut away along the mid-rib, and the halves still attached to the mid-rib were arranged in a large glazed experimental case of the usual pattern, the petioles of each pair of halves dipping into test-tubes of water fixed outside the case. These halves were then placed in strong light of sufficient intensity to cause the leaves to assimilate freely, and a fairly rapid stream of air was drawn through the case, the carbon dioxide taken in by the leaves being estimated in the usual manner.

At the close of the experiment, which lasted some hours, the half-leaves were removed from the case and the mid-ribs were sliced off, the respective areas of the separated laminae and mid-ribs being determined separately by the application of the planimeter to the photographic prints. From the total amount of carbon dioxide assimilated during the experiment a proportional deduction was made for the area of the mid-rib portions which had taken part in the assimilation. The dry weight of the separated laminae was then determined, the final drying taking place in a current of dry hydrogen at 100° C.

Meanwhile, the area and dry weight of the other halves separated at the commencement of the experiment were determined, when we had all the data for determining (1) the increased weight of the leaf-lamina per square decimetre per hour (Sachs' method), and (2) the intake of carbon dioxide and the corresponding amount of carbohydrate produced per square decimetre per hour. The final results of four such experiments are given in the following Table VIII. The areas of leaf employed varied from about 550 to 750 sq. cm.

Table VIII.—Direct Comparison of the Increase in Weight during Insolation of the Leaf-Lamina of *Catalpa bignonioides*, with the Intake of CO<sub>2</sub> from ordinary Air, and the corresponding Amount of Carbohydrate formed.

	Increased weight of leaf-lamina per square decimetre per hour in grammes.	CO <sub>2</sub> absorbed by leaf per square decimetre per hour in cubic centimetres.	Carbohydrate formed per square decimetre per hour deduced from CO <sub>2</sub> absorbed, in grammes.
Experiment (1).....	0·00983	1·41	0·00176
„ (2).....	0·00714	1·43	0·00179
„ (3).....	0·00260	2·35	0·00294
„ (4).....	0·00722	2·33	0·00292
Mean .....	0·00669		0·00235

A comparison of the first and third columns in the above table shows a very considerable discrepancy between these two methods of estimating the rate of assimilation.

In only one case, that of Experiment (3), is there any kind of agreement between the results of the weighing method and that based on intake of carbon dioxide: in all other instances the Sachs' method gives results which are far in excess of the direct method. If we take the mean of all four experiments we find that the Sachs' method gives an estimate of the assimilation rate between two and three times greater than that deduced from the intake of carbon dioxide, a result which agrees fairly well with the previous experiments which were not carried out under conditions admitting of such rigorous comparison as those of Table VIII.

The discrepancy is far too great to be accounted for by any under-estimate of the amount of carbohydrate equivalent to the fixation of a given amount of carbon dioxide, and can only be explained by some error incident to the Sachs' method of determination. This is the more certain since in one experiment, the results of which are not recorded in Table VIII, the apparent dry weight of the leaf-lamina per unit-area was actually *less* after insolation of the leaf than it was before, although there had been an intake of carbon dioxide corresponding to the assimilation of 0·003 gramme per square decimetre per hour.

The great objection to the Sachs' method is that all the various errors to

which it is liable *are accumulative in the result*, and affect that result absolutely. Besides the ordinary errors to which operations of measuring and weighing are liable, and which may be so far reduced as to be almost negligible, there are three possible sources of error which may have a very serious influence on the result. In the first place it is by no means certain that the cell-wells and contents of the leaf-cells after insolation are in the same condition as regards their constitutional water as they were before insolation. We are not referring here to such metabolic changes as those due to the hydrolysis of starch or cane-sugar or the reverse changes, for although such transformations undoubtedly result in the fixation or liberation of water, and theoretically must have an effect on the final dry weight of the leaf, yet it can be shown that this effect must be relatively small. We refer rather to possible changes in the power of retention of water at 100° C. by the colloidal elements of the cell-contents. A very small change in this power of water retention might make a very appreciable difference in the final estimate by the Sachs' method of the apparent amount of matter assimilated; but the two principal sources of error in the Sachs' method, compared with which all others sink into comparative insignificance, are no doubt (1) differences due to want of perfect symmetry in the venation and the thickness of the lamina, and (2) alterations of area in corresponding parts of the leaf, one of which is measured at once, and the other only after being placed in the light for some hours, during which time, although the leaf may apparently remain unaltered, it is put under a different state of tension.

We have made a number of experiments on both these points. In the first place, in investigating the degree of symmetry which exists on the two sides of a leaf, only those leaves were taken which appeared to the eye to be quite symmetrical. The two sides of the leaf were then separated carefully from the mid-rib, printed on photographic paper, and the area of each approximately equal side carefully taken with the planimeter. We may here mention that errors of planimeter measurement fall well within 0.1 per cent.

The halves of the leaves were then dried under exactly the same conditions in a slow current of dry air until constant in weight.

Another series of experiments was then made in order to estimate the possible difference in area, due to *shrinkage or the reverse*, which a leaf undergoes on insolation. A leaf of *Catalpa bignonioides* was divided down the middle, and the half to which the petiole was still attached was printed on photographic paper, and the area determined with the planimeter. These half-leaves were then placed in a glazed assimilation-case and exposed to sunlight under a canvas screen, air being drawn through the case just

Table IX.—Test of Symmetry between Opposite Sides of Leaves.

R. = Right half. L. = Left half.

Name of plant.	Area in square centimetres.	Dry weight in grammes.	Dry weight per square decimetre in grammes.	Difference, per cent.
<i>Catalpa bignonioides</i> .....	R. 114·32	0·4652	0·4069	
	L. 99·90	0·3906	0·3909	— 3·9
„ „ .....	R. 164·6	0·8482	0·5153	
	L. 155·8	0·7680	0·4929	— 4·3
„ „ .....	R. 126·75	0·6024	0·4752	
	L. 131·27	0·6386	0·4864	+ 2·3
„ „ .....	R. 111·95	0·4211	0·3761	
(This leaf had been depleted by covering)	L. 103·90	0·3685	0·3546	— 5·7
<i>Catalpa bignonioides</i> .....	R. 107·3	0·4983	0·4644	
	L. 108·32	0·4994	0·4610	— 0·7
<i>Catalpa purpurea</i> .....	R. 89·1	0·4526	0·5079	
	L. 90·6	0·4716	0·5184	+ 2·0
<i>Catalpa Bungei</i> .....	R. 112·6	0·6261	0·5560	
	L. 114·8	0·6472	0·5637	+ 1·3
„ „ .....	R. 110·5	0·6504	0·5855	
	L. 96·2	0·5533	0·5751	— 1·7
<i>Tropæolum majus</i> .....	R. 47·00	0·1754	0·3732	
	L. 43·35	0·1624	0·3746	+ 0·3
<i>Polygonum Weyrichii</i> ...	R. 173·1	0·9124	0·5270	
	L. 177·6	0·9252	0·5209	— 0·1
			Mean error...	± 2·2

Table X.—Influence of Exposure of Leaves in altering Area.

Half leaf.	Area before insolation in square centimetres.	Area after insolation in square centimetres.	Difference per cent. induced by insolation.
(1) <i>Catalpa bignonioides</i> .. .....	112·2	108·7	— 3·12
(2) „ „ .....	111·9	113·0	+ 0·98
(3) „ „ .....	138·4	138·9	+ 0·36
(4) „ „ .....	137·1	137·3	+ 0·14
		Mean.....	± 1·1



as in experiments on assimilation. After six hours' exposure the leaves were again printed, and the areas determined afresh.

It will be seen on examining Tables IX and X that the errors which may be introduced into the Sachs' weighing method from the causes there noted may be of considerable magnitude. The average error observed due to differences in symmetry amount to 2·2 per cent. and that due to change of area to 1·1 per cent. Assuming that the accumulated errors from all sources in a Sachs' experiment amounted to 2·0 per cent., with a leaf having a dry weight of 0·50 gramme per square decimetre, this would lead to an over or under-estimate of the matter assimilated of 0·010 gramme per square decimetre for the total time of experiment, and if the duration of the experiment were five hours, to an apparent assimilation or depletion at the rate of 0·002 gramme per decimetre of leaf per hour. But this is about the average amount of true assimilation observed for the leaf of *Catalpa bignonioides* by the direct method of determining the carbon dioxide assimilated, so that an under-estimate of the area of only 2 per cent. in the insolated half-leaves would on the Sachs' weighing method give an over-estimate of the assimilation of 100 per cent. of the true value, whereas it would only affect the results obtained from our method of carbon dioxide absorption to the extent of 2 per cent.

In the light of these experiments we cannot avoid the conclusion that the Sachs' method cannot be trusted for anything like exact quantitative estimation of the photosynthetic work which is going on in an assimilating leaf. As ordinarily applied its general tendency is to give far too high an estimate of the rate of assimilation, which can only be measured with any approach to exactness by a determination of the actual intake of carbon dioxide into the leaf from an atmosphere containing that gas in small and determinate amounts.

Section (3).—*The Relation of the Distribution of Stomata to the Rate of Gaseous Exchange in the Leaf.*

This is a subject which has been very fully and satisfactorily investigated by F. F. Blackman,\* who demonstrated for the first time that the exchange of carbon dioxide between the leaf and the surrounding air closely follows the stomatic distribution on the two surfaces of the leaf, and that the experiments can only be interpreted on the supposition that the gaseous exchanges take place by free diffusion through the open stomates and not by diffusion across the imperforate portions of the leaf-cuticle.

\* 'Phil. Trans.,' vol. 186 (1895), p. 502.

As regards the exhalation of the carbon dioxide of respiration, Blackman's experiments are quite conclusive, but his method does not appear to be quite so well adapted to investigations of the assimilatory intake where, owing to the restrictions of time and leaf area, the amounts of carbon dioxide which have to be dealt with seldom exceed about 0.1 c.c., with a possible experimental error of about one-tenth of this amount, and where the conditions of experiment are such as to require "much watchfulness, and a favourable concurrence of circumstances such as is rarely accorded."

Since the method which we have employed for determining the rate of assimilation in ordinary air is one which readily lends itself to investigations of this nature, we have considered it desirable to repeat these classical experiments of Blackman under conditions which admit of measuring the intake of relatively large amounts of carbon dioxide from ordinary air by the two sides of a leaf on which the distribution of stomata is known.

For this purpose special leaf-cases were constructed which were similar in principle to those described by Blackman.\* They consisted of a pair of shallow Petri-dishes fixed into light brass frames with flanges which could be pressed together by simple spring-clips. When the leaf was clipped between the two flanges and the junction was made tight with soft wax the lamina formed a diaphragm dividing the case into two compartments, one connected with the upper and the other with the lower side of the leaf. Through each of these compartments a separate current of air could be drawn by means of small brass tubes fitted into the sides of the chambers.

Two of these cases were used, one exposing a leaf-area of 28.27 sq. cm., and the other 59.44 sq. cm.

Measured volumes of ordinary air of known carbon dioxide content were aspirated through the cases in the way already described at rates varying from 10 to 20 litres per hour, the absorption and determination of the carbon dioxide in the emergent air being effected as usual.

The number of stomata on known areas of the upper and lower sides of the leaf was, in all cases determined under the microscope by actual counting, the mean of a large number of observations being taken.

In order to make the comparison as strict a one as possible the results of each pair of experiments have been reduced to equal partial pressures of carbon dioxide in the air passing through the case. Such a correction is very necessary in experiments on respiration in which there is sometimes a considerable difference in the mean composition of the air in the two compartments.

\* *Loc. cit.*, p. 521.

Table XI.—Respiration of Amphistomatous Leaves showing Relation of Carbon Dioxide evolved by Upper and Lower Surface, and Ratio of Distribution of Stomata.

U. = Upper surface. L. = Lower surface.

Plant.	Time in hours.	Leaf area in square centimetres.	CO <sub>2</sub> evolved in cubic centimetres.	Ratio of CO <sub>2</sub> evolved. $\frac{\text{Upper}}{\text{Lower}}$ .	Ratio of stomatic distribution. $\frac{\text{Upper}}{\text{Lower}}$ .
(1) <i>Canna indica</i> ...	4.75	28.27	U. 8.41 L. 20.76	100 <u>246</u>	100 <u>246</u>
(2) " " ...	5.0	28.27	U. 5.55 L. 17.90	100 <u>322</u>	100 <u>246</u>
(3) " " ...	4.23	28.27	U. 3.04 L. 6.40	100 <u>210</u>	100 <u>246</u>
(4) <i>Rumex alpinum</i>	5.5	59.44	U. 1.03 L. 3.60	100 <u>286</u>	100 <u>269</u>

Table XII.—Assimilation of Amphistomatous Leaves illuminated on Upper Surface, showing Relation of Intake of Carbon Dioxide by the Upper and Lower Sides and the Ratio of Distribution of Stomata.

U. = Upper side. L. = Lower side.

Plant.	Time in hours.	Leaf area in square centimetres.	CO <sub>2</sub> assimilated, in cubic centimetres.	Ratio of CO <sub>2</sub> assimilated. $\frac{\text{Upper}}{\text{Lower}}$ .	Ratio of stomatic distribution. $\frac{\text{Upper}}{\text{Lower}}$ .
(1) <i>Colchicum speciosum</i> ...	5.75	59.44	U. 4.34 L. 3.26	100 <u>72</u>	100 <u>119</u>
(2) <i>Senecio macrophyllum</i> ...	4.75	28.27	U. 3.90 L. 3.60	100 <u>92</u>	100 <u>126</u>
(3) " " ...	4.25	28.27	U. 5.80 L. 4.20	100 <u>72</u>	100 <u>126</u>
(4) <i>Rumex alpinum</i> .....	5.0	59.44	U. 5.70 L. 8.90	100 <u>144</u>	100 <u>269</u>
(5) " " .....	5.5	59.44	U. 7.50 L. 9.81	100 <u>130</u>	100 <u>269</u>

In the following Table XIII are recorded the results of two assimilatory experiments on leaves which have their stomata on one side only. In *Nuphar* the stomates are on the upper, and in *Catalpa* on the lower side of the leaf.

Table XIII.

Plant.	Time in hours.	Area in square centi- metres.	CO <sub>2</sub> assimilated, in cubic centimetres.
(1) <i>Nuphar advena</i> (hyperstomatous) .....	2·0	76·97	U. 2·20 L. 0·00
(2) <i>Catalpa bignonioides</i> (hypostomatous)	1·85	79·03	U. 0·00 L. 4·91
(3)     "           "           "	2·3	79·03	U. 0·00 L. 8·96

The results fully confirm in most respects the observations of Blackman, and may be summarized as follows:—

(1). In the *respiration* of amphistomatous leaves (*e.g.*, *Canna indica* and *Rumex alpinum*, see Table XI) the ratio of the carbon dioxide evolved from the upper and lower surface of the leaf follows very closely the ratio of the distribution of stomates.

(2). In the *assimilatory process* of amphistomatous leaves illuminated on the upper surface (see Table XIII), the intake of carbon dioxide by the lower surface is always *less* than might be expected from the relative number of stomata on the two sides, the amount of carbon dioxide assimilated by the under side in some cases falling to half that deduced from a consideration of the stomatic distribution.

(3). If the leaf is hypostomatous (*vide Catalpa*, Table XIII), the intake of carbon dioxide during assimilation only takes place on the *lower* (stomatiferous) surface.

(4). When the leaf is hyperstomatous (*vide Nuphar*, Table XIII), the intake of carbon dioxide is only on the upper (stomatiferous) surface.

That there should be a much closer correspondence between the ratios of stomatic distribution and the ratios of gaseous exchange in the respiratory than in the assimilatory process, follows from what we know of the physics of diffusion through fine apertures.

Assuming that there is a steady evolution of carbon dioxide going on

in the leaf-cells during respiration, the rate at which this will diffuse into the surrounding air will be quite independent of the degree of opening of the stomata. If the stomata partially close whilst this outward diffusion is going on, the partial pressure of the carbon dioxide within the leaf will increase, and this increase will be inversely proportional to the altered linear dimensions of the opening. This rise in "diffusion potential" will, consequently, exactly counterbalance the effect of the diminished size of the stomatic opening, and *the same amount of respiratory carbon dioxide will consequently escape from the leaf, no matter what changes in the size of the opening takes place*, provided these are not sufficient to close the stomata completely.

This however does not apply to the intake of atmospheric carbon dioxide into the leaf during the assimilatory process. Providing a sufficient amount of the right grade of energy is reaching the chloroplasts, the "diffusion potential" in this case will remain constant, the partial pressure of the inward diffusing carbon dioxide varying from  $3/10,000$  of an atmosphere outside the leaf to zero at the point where complete absorption takes place. Under these conditions the intake of carbon dioxide during assimilation must vary directly with the linear dimensions of the openings. Hence in an amphistomatous leaf the relative rate of assimilation by the two sides will not only be influenced by the number of stomata on equal areas in each case, but also on the degree to which these stomata are opened, a condition which, as we have seen, is not operative in the gaseous exchange of carbon dioxide in respiration.

Partial opening of the stomata on the upper side is extremely likely to be brought about when the incidence of illumination and radiant energy is on that side of the leaf, and in such a case we might expect exactly the results which are recorded in Table XII. There is, however, another factor which no doubt contributes to the apparent excess of assimilation by the upper surface of such leaves. By far the greater part of the particular grade of radiant energy which produces photosynthesis is doubtless absorbed by the chloroplasts of the palisade parenchyma into which the stomata of the upper side of the leaf open. The diffusion gradient will therefore be "steeper" in the intercellular spaces of the palisade parenchyma than in those of the more deeply seated spongy parenchyma, a fact which will in itself favour a more rapid inflow of carbon dioxide into the leaf through the stomata of the upper side.

Section (4).—(a) *Experiments on Leaves Exposed to Artificial Illumination in a Current of Ordinary Air.*

These experiments were made during the winter months of 1900–1901 with cut leaves of greenhouse-plants illuminated on the upper sides with light from a large No. 4 Welsbach burner.

They were instituted with the idea of working out the influence of varying external conditions on the assimilatory process under constant illumination, but failed in this object owing to the comparatively feeble photosynthetic power of the source of light used, and the abnormal respiration which occurs at this time of the year in greenhouse-plants. These two causes resulted in a complete masking of the assimilatory process as measured in the ordinary way, the air which had been in contact with the leaf always gaining in carbon dioxide owing to respiration being in excess of assimilation.

More satisfactory results would, no doubt, have been obtained by this method in the summer, but this line of research was abandoned when it was found that definite variations in the intensity of sunlight or diffused daylight could be conveniently produced by the revolving radial sectors already described, thus admitting of comparisons being made in simultaneous experiments lasting for some hours, although the actual intensity of the unobstructed radiation might vary considerably during that time.

Nevertheless some of these experiments with artificial illumination are not devoid of interest, and we have, therefore, briefly alluded to a few of them.

The actual heating effect\* of a large Welsbach burner placed within a foot or two of a leaf enclosed in its glazed case is considerable, and had to be neutralised as far as possible by passing the light through a water-cell 2 or 3 inches in thickness. Where comparisons were made with the respiration effect in darkness, the respiratory chamber was as far as possible brought to the same temperature as the one in which the assimilatory effect was investigated.

The leaf was enclosed as usual in its case through which a measured stream of air was aspirated, of which the carbon dioxide-content was determined at ingress and egress, and the case was suitably arranged so that no light could reach the leaf except that coming from the gas burner.

The temperature of the air in the case was given by a thermometer inserted

\* The total radiation from the Welsbach burner employed, at a distance of 1 foot and with only a thin glass screen, was found by the Callendar's radiometer to be 0·089 cal. per sq. cm. per minute. When the water-cell was interposed this fell to 0·031 cal. per sq. cm. per minute. At a distance of 2 feet these values were, of course, reduced to one quarter.

through the side, and since a fairly rapid stream of air was passing through the apparatus, and the leaf was under favourable conditions for transpiration, it is almost certain that the temperature of the leaf cannot have been far removed from that of the air surrounding it.

Table XIV.—Experiments on Leaves illuminated by Welsbach Light.

Name of plant.	Distance of source of light from leaf in feet.	Temperature, C.	Area of leaf in square centimetres.	Duration of experiment in hours.	CO <sub>2</sub> evolved during experiment in cubic centimetres.	CO <sub>2</sub> evolved per square decimetre per hour in cubic centimetres.
December 25— <i>Dioscorea cayennensis</i> .						
(1) A. In darkness...	—	19°·1	200·0	2·2	40·30	9·16
B. Illuminated...	1	22°·3	—	2·3	33·58	7·30
January 10— <i>Dioscorea cayennensis</i> .						
(2) A. In darkness...	—	19°·9	169·4	2·8	36·35	7·662
B. Illuminated...	1	22°·7	—	2·55	22·17	5·129

Partial re-assimilation of the carbon dioxide of respiration has evidently taken place in both instances under the influence of the artificial illumination, in (1) to the extent of about 1·86 c.c. per sq. decimetre per hour, and in (2) to the extent of about 2·53 c.c. These it is true are amounts which compare favourably with the rate of assimilation of leaves exposed to sunlight in ordinary air containing the normal amount of carbon dioxide, but we are certainly not justified in deducing that the Welsbach light is rich in photosynthesizing rays, since the conditions are widely different. In ordinary air the maximal partial pressure of the carbon dioxide surrounding the assimilating centres must fall considerably short of 3/10,000 of an atmosphere, whereas during active respiration the air of the intercellular spaces may be highly charged with that gas, thus increasing the assimilatory effect in proportion. In the former case the limiting factor is the small partial pressure of the carbon dioxide, the photosynthetic rays being in excess; whilst in the latter case the limitation is due to the comparative want of a sufficient amount of radiant energy of the right kind, and not to paucity of carbon dioxide.

That this is the true explanation was shown by another experiment on one of these very actively respiring leaves of *Dioscorea* by illuminating it in the

laboratory with feeble winter sunlight, when the amount of carbon dioxide evolved fell to 0·28 c.c. per square decimetre per hour.

(b) *Experiments on Respiration.*

The abnormal respiratory effect observed in greenhouse plants during the winter months is shown in the following Table XV, and in Table XVI we have shown by way of contrast the normal respiration observed in certain leaves during the *summer*, the plants in this instance having been grown under ordinary out-door conditions.

Table XV.—Winter Respiration of the Leaves of Greenhouse-plants.

Date.	Name of plant.	Temperature, C.	CO <sub>2</sub> respired per square decimetre per hour in cubic centimetres.
December 14.....	<i>Senecio grandifolius</i>	25°·2	5·12
„ 20.....	<i>Dioscorea cayennensis</i>	22°·7	13·45
„ 26.....	„ „	19°·0	8·78
„ 5.....	„ „	19°·9	5·33
„ 12.....	<i>Plumeria lutea</i> .....	19°·7	2·49
„ 7.....	<i>Begonia haagiana</i> ...	16°·5	3·38
„ 13.....	<i>Sapium bolinense</i> .....	18°·7	8·98

Table XVI.—Summer Respiration of Leaves grown under Out-door Conditions.

Date.	Name of plant.	Tempera- ture, C.	CO <sub>2</sub> respired per square decimetre per hour in cubic centimetres.
August 22 .....	<i>Helianthus annuus</i> ...	24°·1	0·429
September 7 .....	„ „ .....	26°·8	0·714
June 26 .....	<i>Petasites albus</i> .....	18°·0	0·321
July 5 .....	„ „ .....	25°·6	0·584
June 22 .....	<i>Polygonum Weyrichii</i>	17°·8	0·721
July 3 .....	„ „	25°·2	0·788
July 11 .....	„ „	36°·4	1·179

It will be noticed that, except in the last instance, where the temperature was very high in the respiration case, the respiration of these leaves growing under normal out-door conditions does not average more than 6/10 c.c. of



carbon dioxide per square decimetre of leaf per hour, or less than one-tenth of the amount observed in the winter respiration of the greenhouse plants.

The influence of increased temperature in accelerating respiration is, as is well known, very considerable. This is illustrated in a general way by the following experiments made in the summer of 1900 on leaves of *Helianthus annuus* whilst still attached to the plant.

Table XVII.—Influence of Temperature on the Respiration of Leaves of  
*Helianthus annuus*.

Temperature, C.	CO <sub>2</sub> respired per square decimetre per hour in cubic centimetres.
19°·6	0·579
31°·2	1·656
36°·3	1·839
39°·2	2·080
41°·7	2·451

The above experiments are not strictly comparable, since they were made on different leaves of the same plant and on different days. A more complete series was made in a darkened glass cylinder immersed in water which was kept at a constantly regulated temperature, but the record of this experiment has been lost.

### PART III.—THE ENERGETICS OF THE LEAF.

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#### Section (1)—*General Considerations of the Thermal Relations of a Leaf to its surroundings.*

Before we can profitably discuss the general question of the exchange of energy between a living leaf and its environment, it is necessary to

consider those physical and chemical changes occurring within the leaf which are attended by any sensible evolution or absorption of energy.

Of these there are only three which need be taken into serious account ; (1) the vaporization of water ; (2) the photosynthesis of carbohydrates ; and (3) the chemical changes attendant on respiration.

The first two changes are *endothermic* in character, but are as a rule of very dissimilar value as regards the actual thermal disturbances induced, (1) under ordinary circumstances being very large compared with (2).

The respiratory changes (3) are *exothermic* in their final result.

By suitable means the loss or gain of heat due to each of the above-mentioned changes can be determined in water-gramme units, and referred to the total amount of energy received by the leaf from its surroundings, either through radiation or the convective and conductive action of the air. In order, however, to complete our knowledge of the thermal relations of leaf and environment, we must know something of the absorptive power of the leaf-lamina for the particular form of radiant energy incident upon it, and also its *thermal emissivity*, using that term in its wide sense to include the loss or gain of heat due to radiation and air-convection and conduction which unit-area of the leaf will experience in unit-time, with unit difference of temperature between itself and its surroundings. In some cases we also require to know the weight of unit-area of the lamina and its approximate specific heat. Our investigations, described in detail later on, have led us to fairly accurate methods for the determination of all these factors.

For some time the story could not be made complete, owing to difficulties in determining the *thermal emissivity* of a leaf. These difficulties have now been surmounted by the adoption of a comparatively simple method based on the differential self-cooling of leaves which are transpiring at unequal rates. The method is fully described in a separate communication.\*

As a preliminary to the study of the thermal interchanges between a leaf and its surroundings, it will be convenient to consider two distinct sets of general conditions ; (A) when the leaf is shaded from direct solar radiation or any other form of radiation which can produce photosynthesis ; and (B) when the leaf is receiving solar radiation.

Case A.—*The Thermal Relations of a Leaf to its Surroundings when it is shielded from Solar Radiation.*

In order as far as possible to simplify the problem, we will assume in this case that a detached leaf, freely supplied with water, is placed in an enclosure,

\* See Brown and Wilson, *infra*, p. 122.

the walls of which are non-reflective and are maintained along with the enclosed air, at a perfectly uniform temperature which we will denote by  $\theta$ . We will further assume that at the commencement of the experiment the leaf is also at this same temperature  $\theta$ .

If the air of the enclosure is saturated with water-vapour, and there are no chemical changes going on in the leaf attended with evolution or absorption of energy, there will be complete thermal equilibrium in the system, all parts of which will remain at temperature  $\theta$ .\*

Since, however, active respiration is going on in the leaf-cells, this static thermal condition cannot be exactly maintained, and the leaf-lamina will consequently tend to rise slightly in temperature.

How small is the thermal disturbance due to this cause will be apparent from the following considerations.

The amount of carbon dioxide evolved is a measure of the oxidation of the leaf-substance used up in the respiratory process, hence, provided we know the nature of the oxidized substance, and its heat of combustion in absolute units, we can determine the liberated energy corresponding to the appearance of a given amount of carbon dioxide per unit-area of leaf per unit-time.

We may safely assume that the substance which is used up in respiration belongs to the class of carbohydrates. Direct evidence of this has been given by Brown and Morris,† who found that the disappearance of the sugars and starch of leaves of *Tropæolum* placed in the dark corresponded very closely with the loss of weight due to respiration.‡

The heat of combustion of the different carbohydrates for equal weights of contained carbon varies only within narrow limits, and we may therefore, without serious error, safely refer the carbon dioxide of leaf-respiration to a sugar of the *hexose* class, having a heat of combustion of about 3760 calories per gramme.

The actual amount of carbon dioxide respired by a leaf varies considerably

\* It is here assumed that the partial pressure of the water-vapour in the interspaces of the leaf is in equilibrium with the vapour-pressure of a *plane surface* of water at the same temperature. Should it ever be proved that transpiration into a saturated atmosphere is really possible when the whole system is in perfect thermal equilibrium, the cause must be sought either in the increased vapour-pressure of minute convex surfaces, such as give rise to the distillation of small drops into large ones, or, in some such properties of colloids, as those suggested by the observations of J. M. van Bemmelen and v. Schröder, which indicate that a higher tension of water-vapour can be maintained over a "gel" than corresponds to a plane surface of water at the same temperature.

† 'Journ. Chem. Soc. Trans.,' 1893, p. 671.

‡ Compare also the results of T. C. Day ('Journ. Chem. Soc. Trans.,' 1880, p. 658), who showed that the ratio of the carbon dioxide and water liberated during the germination of barley corresponds closely with that required for the combustion of a glucose.

with the temperature and with the age and species of the plant. At about  $20^{\circ}\text{C.}$ , we have found healthy mature leaves of *Helianthus annuus* evolve about 0.70 c.c. of carbon dioxide per square decimetre of leaf-lamina per hour, or 0.000116 c.c. per square centimetre per minute. This corresponds to  $1.55 \times 10^{-7}$  gramme of dextrose, or to an evolution of heat of  $1.55 \times 10^{-7} \times 3760 = 0.000582$  calorie per square centimetre of leaf-lamina per minute.

Since the weight of one square centimetre of the leaf-lamina of *Helianthus* is about 0.020 gramme, and its specific heat is about 0.879 (water = 1.0) the above amount of heat of respiration would be sufficient to raise the temperature of the leaf at the rate of  $0^{\circ}.033\text{ C.}$  per minute, *provided no simultaneous loss of heat were taking place by radiation, air-convection, or internal work of vaporization.*

But all these sources of loss of heat become operative directly the leaf temperature rises above  $\theta$ , that of its surroundings, and the leaf can only come into thermal equilibrium with its surroundings at some temperature  $\theta_*$  higher than  $\theta$ , at which point the heat of respiration produced in unit-time just balances the sum of the thermal losses due to radiation, convection, and water vaporization.

Before we can estimate the actual rise of temperature of the leaf under the conditions postulated, we must be in a position to determine the rate of loss of energy due to each one of these causes. We will assume first of all that transpiration is still in abeyance, and that the loss of the evolved energy of respiration is due merely to radiation, air-convection, and air-conduction.

From the results given in another paper\* we know that the *thermal emissivity* of the leaf per square centimetre of leaf-surface for "still air," conditions and for a temperature-excess in the leaf over its surroundings of  $1^{\circ}\text{C.}$ , is about 0.015 calorie per square centimetre per minute. This "rate of cooling" has, of course, to be doubled for the two sides of the leaf, so that the emissivity of a square centimetre of leaf-lamina under the above conditions amounts to 0.030 calorie per minute per  $1^{\circ}\text{C.}$  excess.

Since the heat of respiration has been shown to be 0.000582 calorie per minute per square centimetre, the temperature which the leaf will attain when it is in thermal equilibrium with its surroundings will be given by dividing this number by the emissivity-factor, *i.e.*  $\frac{0.000582}{0.030} = 0^{\circ}.019\text{ C.}$

This is the maximal excess temperature above its surroundings to which the leaf can be raised under "still air" conditions when it is respiring 0.7 c.c. of carbon dioxide per square decimetre per hour, provided transpiration still

\* Brown and Wilson, *infra*, p. 122.

remains in abeyance; and this temperature-excess will increase *pari passu* with any increase in the respiratory process. Since, however, any rise of temperature in the leaf, no matter how small, will increase the partial pressure of the water-vapour in the interspaces of the leaf, a diffusion potential will be produced, and water-vapour will flow from the leaf into the surrounding air, hence even this small theoretical maximum will never be reached.

The effect of *transpiration* on the leaf temperature can be best studied in a general way by supposing the leaf to be under the same conditions as above, but surrounded by air which is *not fully saturated* with aqueous vapour for the temperature  $\theta$ ; and here again, for the purpose of argument, we will assume that at the commencement there is no difference of temperature between the leaf and its surroundings.

These conditions are manifestly *unstable* as a consequence of the excess of the partial pressure of the saturated air of the leaf-interspaces over the partial pressure of the water-vapour in the unsaturated air of the enclosure. Owing to the "diffusion-potential" thus set up water-vapour will diffuse through the stomata if these are in any degree open, and the temperature of the leaf will fall. This will continue until the temperature-gradient between the leaf and its surroundings is steep enough to allow energy to flow into the leaf from without at a rate equal to that of the energy expended in the work of vaporization. A thermal static state will then be re-established which will remain constant as long as the conditions remain unaltered, the leaf assuming a temperature  $\theta_n$ , which will be *less* than  $\theta$ , the temperature of the surroundings.

Neglecting for the moment the very slight disturbance due to the exothermic respiratory process, as soon as the above thermal equilibrium has been attained *the amount of water, Q, lost by unit-area of the leaf surface in unit-time, is a measure of the energy flowing into the leaf from its surroundings*, and if we know the temperature difference between the leaf and its surroundings, *i.e.*, the temperature gradient  $\theta - \theta_n$  we can determine the rate of interchange of energy between the leaf and its surroundings in absolute units for a temperature difference of  $1^\circ \text{C.}$ , that is to say, the *coefficient of thermal emissivity*.

This method of determining the emissivity to which reference has already been made, is elaborated in an accompanying paper.\* When once the constant of emissivity has been determined the value of the temperature difference  $\theta - \theta_n$  is calculable, providing we know Q, the amount of water transpired by the leaf for unit-area and unit-time.

\* Brown and Wilson, *infra*, p. 122.

As a concrete example of a leaf transpiring in an enclosure under the conditions just postulated, we will assume that the leaf is losing water steadily at the rate of 0.5 gramme per square decimetre per hour, or 0.0000833 gramme per square centimetre per minute. The heat required to vaporize this last-mentioned amount of water at 20° C. is  $0.0000833 \times 592.6 = 0.04938$  water-gramme-units (calories), and, excluding the small disturbance of the respiratory process, this must represent, according to the theory of exchanges, the amount of energy entering and leaving a square centimetre of the leaf-lamina in one minute, when the steady thermal state has been attained. If the leaf has a thermal emissivity of 0.015 calorie per square centimetre of leaf *surface* per minute for a 1° C. temperature gradient, the temperature difference,  $\theta - \theta_n$ , between the leaf-lamina and its surroundings will be  $\frac{0.04938}{2 \times 0.015} = 1.64$  C., when the leaf is transpiring at the rate of 0.5 gramme per decimetre per hour, under "still air" conditions.\*

Case B.—*Thermal Relations of a Leaf to its Surroundings when it is  
Receiving direct Solar Radiation.*

The experimental data which are required for an investigation of the energetics of a leaf receiving direct solar radiation, in addition to those already made use of in Case A (see p. 70), are as follows: (1) The total amount of solar radiant energy incident on a given area of the leaf in a given time; (2) the amount of this radiant energy which is absorbed by the leaf (coefficient of absorption); (3) a measure of the internal work of the leaf due to (a) water-vaporization, and (b) photosynthesis; and (4) the influence which air currents of definite velocity exercise on the thermal emissivity of the leaf surface.

The total solar radiation falling on the leaf was measured by means of a Callendar's radiometer which was connected with a Callendar's self-recorder. The radiometer was calibrated in water-gramme-units and was placed beside the leaf under experiment with similar orientation. The integration of the thermal curve recorded on the drum was performed by an attached planimeter, the reading of which gave a measure of the average solar radiation falling on unit-area of the leaf in unit-time for the whole period during which the experiment lasted.

The coefficient of absorption of the leaf for solar radiation was determined by means of the same instrument in the manner described in detail later on. It

\* The influence of movement in the air in increasing the thermal emissivity and in decreasing the temperature difference  $\theta - \theta_n$  will be considered later.

was taken as the difference between the solar radiant energy falling on the leaf in full sunshine and the amount transmitted, and takes no account of any possible *reflection* of radiation from the surface of the leaf. With perpendicular incidence the reflected radiation must be very small in amount, but it is well to bear in mind that, strictly speaking, the value of the coefficient of absorption employed includes this reflected portion. Although the absorptivity varies in the leaves of different plants there is a remarkable constancy in the results obtained at different times with the leaves of plants of the same species.

The loss of water by the leaves due to transpiration was determined by weighing the leaf and its attached water-tube at suitable intervals.

In those cases where it was desired to submit two leaves to solar radiation of definite relative intensity, the leaf to be partially shaded was placed under the radial arms of a *revolving sector* which could be adjusted for any required degree of "exposure." In this way a leaf could be submitted to a definite fraction of the full solar radiation falling on another leaf placed alongside without the risk of introducing any error from selective absorption of any special rays, which it is difficult to avoid when ordinary screens are used. The area of the leaves was ascertained by the planimeter method described in an earlier part of the paper, and the amount of energy used up in the photosynthetic process was deduced from the rate of assimilation as determined by the absorption of carbon dioxide from the air, a method which has been fully described in Part II.

Before discussing the results of some typical experiments it will be well to consider in a general way the thermal relations of a leaf to its surroundings when it is exposed to sunlight under free air conditions, just as we have considered these relations in the case of a leaf under the still air conditions of an enclosed space cut off from direct solar radiation.

In the first place let us suppose a healthy green leaf, well supplied with water, to be exposed to sunlight under perfectly constant conditions as regards intensity of solar radiation, and the temperature, humidity and degree of movement in the surrounding air; and further that the apertures of the stomata undergo no variation in dimensions. Under these ideal conditions, just as in the case previously considered, a state of thermal equilibrium will be speedily established between the leaf and its surroundings, when the loss and gain of energy by the leaf in a given interval of time will just balance.

Let  $R$  represent the total solar radiation expressed in water-gramme-units (calories) falling on a square centimetre of the leaf-lamina in one minute, and let  $a$  represent the "absorptive coefficient" of the leaf for this radiation.

Then  $Ra$  will represent the radiant energy absorbed per square centimetre of leaf-lamina per minute.

It is worth while at this point to see how the temperature of the leaf would be affected on the assumption that none of this absorbed energy were dissipated. If we denote the mass of a square centimetre of the leaf-lamina by  $m$ , and its specific heat by  $s$ , the rise of temperature of the leaf-lamina per minute will be represented by  $Ra/ms$ .

Taking  $R$ , the solar radiation, at the comparatively low value of 0.8 calorie per square centimetre per minute,  $a$ , "the coefficient of absorption" of the leaf as 0.78,  $m$  the weight of a square centimetre of leaf as 0.020 gramme, and  $s$  its specific heat as 0.879; then the rise of the temperature of the leaf under the conditions postulated would be  $\frac{0.8 \times 0.78}{0.02 \times 0.879} = 35^{\circ}.4$  C. *per minute*, a result which would be speedily fatal to the leaf if there were no means of dissipating the absorbed radiation.

The dissipation of energy necessary to keep within safe limits the temperature of a leaf exposed even to moderate solar radiation is provided for by the internal work performed, and by the loss of heat due to radiation and air-convection. The internal work attended with any sensible absorption of energy is (1) vaporization of water, and (2) photosynthesis of carbohydrates from atmospheric carbon dioxide.

We have a measure of (1) in the water lost by transpiration, and denoting this loss per square centimetre of leaf-lamina per minute by  $Q$ , the heat dissipated by vaporization for the same units of leaf-area and time will be **592.6  $Q$**  calories; 592.6 being the latent heat of vaporization of 1 gramme of water in water-gramme-units.\*

The energy used up in photosynthesis can be determined from the mass or volume of carbon dioxide absorbed by the leaf under the conditions of the experiment.

The heat of combustion, and therefore with a reversed sign, the heat of formation of the carbohydrate synthesized, must closely approximate 3760 calories per gramme, hence it can readily be shown that the assimilation of 1 cubic centimetre of carbon dioxide, measured at normal temperature and pressure, corresponds to 0.001336 gramme of a hexose, and to the absorption of  $0.001336 \times 3760 = 5.02$  water-gramme-units of energy. If, therefore, we denote the volume in cubic centimetres of carbon dioxide assimilated by

\* This is the latent heat of vaporization of water at  $20^{\circ}$  C. The value varies slightly with the temperature, according to the formula  $606.5 - 0.695 t^{\circ}$ ,  $t^{\circ}$  being the temperature in degrees Centigrade.



1 square centimetre of leaf-lamina per minute by  $e$ , then the energy used up in photosynthesis, expressed in calories per square centimetre of lamina per minute will be  $5.02e$ .

The total internal work due to water vaporization and assimilation together, per square centimetre of leaf-lamina per minute, will therefore be represented in calories by

$$592.6 Q + 5.02e = W + w,$$

$W$  being the generalized expression for the work effected in water-vaporization, and  $w$  that due to the photosynthetic process.

Now  $W + w$ , owing to the complex interactions of a variety of conditions, may be equal to  $Ra$ , the total solar radiation absorbed by the leaf, or it may be less or greater than this value.

If  $Ra = W + w$  it is evident that when the steady thermal condition is attained, the leaf will have the same temperature as its surroundings.

If, on the other hand,  $Ra$  exceeds  $(W + w)$ , then the excess of solar radiant energy will raise the temperature of the leaf above that of its surroundings, and the steady thermal condition will only be attained when there is a sufficiently high temperature gradient for the excess of energy thus received, to be dissipated by re-radiation and convective cooling. The thermal static condition will in this case be represented by

$$Ra = (W + w) + r,$$

$r$ , being a measure in calories of the sum of the losses due to radiation and convective cooling, whilst at the same time it is the only portion of  $R$  which can produce a rise of temperature in the leaf. It will be observed that whilst  $Ra$  and  $(W + w)$  are values obtained by direct experiment,  $r$  is a difference value.

The actual rise of temperature of the leaf above its surroundings can be determined from  $r$  if we know the *thermal emissivity* of the leaf surface, which is ascertainable. If  $e$  is taken to represent this emissivity in air in calories per square centimetre of leaf *surface*\* per minute, for a difference of  $1^\circ$  between the leaf and its surroundings and, as before,  $\theta$  = the temperature of the surroundings, and  $\theta_n$  that of the leaf, then, when the thermal static state is attained, the temperature difference  $\theta_n - \theta = r/2e$ .

We have still to consider the case when  $Ra$ , the absorbed solar radiation,

\* Care must be taken to differentiate between the "area of leaf-lamina" and the "surface-area of a leaf." In the above equations  $R$ ,  $W$ ,  $w$ , and  $r$  are in terms of the former, whilst  $e$  is in terms of "surface-area" and has, therefore, to be multiplied by two when used for determinations of the temperature of the lamina.

is *less* than  $W + w$ , representing the sum of the internal work of the leaf. The equation for static thermal equilibrium then becomes

$$Ra + r = W + w.$$

The excess amount of energy requisite for producing the internal work under these conditions *must be drawn from the surroundings of the leaf*, that is to say, the temperature of the leaf must fall below that of its surroundings when thermal equilibrium is reached. The thermometric difference  $\theta - \theta_n$  will again be expressed by  $r/2c$ , as in the preceding case.

The influence of the heat evolved by the respiratory process has still to be considered. The true measure of the photosynthetic work effected by suitable radiation is, strictly speaking, not given by the amount of atmospheric carbon dioxide absorbed by the leaf, but by this amount *plus* the carbon dioxide which would have been evolved by respiration if photosynthesis were in abeyance. But this correction, although one to be taken into account under certain circumstances, does not affect the above thermal equations, since the heat of respiration is opposite in sign to the heat of reformation of the carbohydrate, and these values, representing a concurrent gain and loss of energy by the leaf, must exactly balance each other if the two carbohydrates are identical; and if they are not identical the difference will be so extremely small that it may be safely neglected.

In discussing the thermal relations of a leaf to its surroundings we have so far, for the sake of simplicity, imagined an ideal set of conditions under which all the determining factors, both internal and external, remain constant for a sufficient time to allow of the attainment of static thermal equilibrium. In practice this ideal condition is never attainable. In the first place the incidence of solar radiation, even under the most fair-weather conditions, is subject to rapid oscillations of considerable magnitude, as can readily be seen by watching the constant movement of the pen of the self-recording instrument or by reference to the final "graph" which is integrated by the attached planimeter.

Every variation of this kind alters the value of  $Ra$ , the actual amount of energy absorbed by the leaf. Even if these changes are unaccompanied by any alteration in the degree of opening of the stomata, and the external air conditions remain constant, the amount of water vaporization must still be indirectly influenced, since the value of  $r$  which represents the difference between the amount of the utilizable incident energy and the internal work performed, must also vary, and as this determines the temperature of the leaf, there will be corresponding changes in the "diffusion-potential" between the inner saturated air of the leaf and the surrounding atmosphere.

Should the variations in solar radiation produce directly or indirectly any effect on the guard-cells which control the stomatic openings, there will be a consequent increase or decrease in transpiration due to this cause, and this will again produce its effect on  $W$  and  $r$ . The same will also be true of any variation in the hygrometric state of the outer air, and of the slightest change in its temperature. But of even more importance than any of the above mentioned disturbing factors is the influence exerted by variations in the velocity of the air-currents passing over the leaf. These variations act mainly through their effect on the *thermal emissivity* of the leaf,  $e$ , and have been the subject of a special investigation\* which brings out the important fact that the thermal emissivity of a leaf increases over "still air" conditions by about 0.0017 calorie per square centimetre of leaf surface per minute for every increase in the velocity of 10 metres per minute. Thus a leaf which has an emissivity in still air of 0.015 calorie per square centimetre of leaf surface per minute for a temperature excess of  $1^{\circ}$  will have this *doubled* by the very moderate air-velocity of 44.2 metres per minute (2.65 kilometres per hour) and trebled at double this velocity. It only requires reference to the formula connecting leaf-temperature with emissivity to see that this would mean a corresponding diminution of the leaf-temperature to one-half and one-third respectively of that in still air, when all other conditions remain the same.

But in addition to the influence of moving air-currents on the "rate of cooling" of the leaf induced by alterations in the thermal emissivity of its two surfaces we have also to consider the direct effect of the currents in promoting transpiration, and here we must draw attention to one very essential point of difference between the loss of water from the surface of an actively transpiring leaf and evaporation from a free surface of water. The difference is one of fundamental importance to the well-being of the leaf and depends on its physical structure. If we imagine a free limited surface of water exposed to evaporation in unsaturated air which is in very slight steady horizontal movement,† the partial pressure of the water-vapour in the air may be regarded as varying in a direction normal to the surface of the liquid from a maximum of  $p_1$  at the immediate surface to a partial pressure of  $p$  at some distance  $l$  above the surface,  $p$  expressing the partial pressure ("tension") of the water-vapour in the surrounding air before it comes under the influence

\* See Brown and Wilson, *infra*, p. 122.

† For the sake of simplicity we have imagined the air to be in very slight movement just sufficient to displace the curved lines of equal density of the over-lying water-vapour and to render these practically horizontal. The exact form which the lines of equidensity would take in perfectly still air over a circular disk of liquid has been fully discussed elsewhere (see Brown and Escombe, 'Phil. Trans.,' B, vol. 193, 1900, p. 223).

of the evaporating liquid. The gradient of density on which, other things being equal, the rate of evaporation depends, is represented by  $(\rho_1 - \rho)/l$  so that an increased velocity of the air-current over the liquid surface will *increase the speed of evaporation* by reducing the value of  $l$ . This will take place no matter whether the air is moving across the surface of the liquid in a steady stream, or in a turbulent current with vortices, but in the latter case  $l$  will assume different values in a plane parallel to the surface of the liquid.

There would seem to be no theoretical limit to the increased evaporative power of the air-stream for a given difference of  $\rho_1$  and  $\rho$ , until the speed of the air approaches that of the "mean square speed" of the molecules of water leaving the surface, but no doubt other disturbing factors would come in long before this point was reached. It is sufficient for our present purpose to note that, for all ordinary velocities of atmospheric currents, evaporation from a free water surface will be increased by increased speed of the air-current, a deduction which is consonant with known facts.

The loss of water from the surface of a *transpiring leaf* on the other hand does not take place from a free liquid surface, but by stomatal diffusion, that is to say, by diffusion through a series of fine perforations in the lamina which may be regarded as very short tubes connected below with the interspaces of the leaf in which the partial pressure of the water-vapour is at a maximum. The conditions of diffusion in a system of this kind, both in still and in moving air, have been fully discussed in a previous paper.\*

In *perfectly still air* the rate of diffusion through a tube of area  $S$  is expressed by  $k\rho S/(l+2x)$ ,  $k$  being the diffusion constant for water-vapour in air,  $\rho$  the density (or partial pressure) of the vapour in the outer air at some point remote from the aperture,  $l$  the length of the tube, and  $x$  its diameter  $\times \frac{1}{2}\pi$ . Under the conditions of perfectly still air a series of elliptical "shells" of vapour of equal density is formed over the stomatal aperture, the density increasing from  $\rho$  at some point remote from the aperture to  $\rho_1$  at the aperture itself. A very slight current of air is sufficient to disturb this system of "shells" and to produce a density approaching that of  $\rho$  at the aperture, when the diffusion of vapour outwards, all other conditions remaining the same, will approximate to  $k\rho S/(l+x)$ , *which it cannot exceed no matter how rapid the air-current may be.*

In a leaf stomate of *Helianthus annuus*  $l=0.0014$  cm., whilst  $x=0.00042$  cm. *i.e.*,  $0.3l$ , from which it follows that the ratio of diffusivity of water-vapour through the stomata in still and moving air will be 1:1.23 as a maximum,

\* 'Phil. Trans.,' B, vol. 193, 1900, pp. 256 to 260.

and this maximum will be attained at comparatively low speeds of air current.\*

But although this statement applies to *stomatal* transpiration, which is responsible for the greater part of the loss of water by the leaf, it is not necessarily true for *cuticular* transpiration which may be more responsive to varying wind velocities. The amount of water brought to the free exterior surface of the cuticle must depend not only on the permeability of the cuticle itself, but also on that of the epidermis and the underlying tissue. The epidermal cells with their large lumina must form a bad water-conducting tissue, especially where they overlie the spongy parenchyma. The recent experiments of Buscalioni and Pollacci† on the absorption of water by collodion-films applied to the surface of the leaf indicate that the portions of the cuticle in apposition to the anticlinal cell-walls of the epidermis absorb more water from below than the other portions, and it seems probable that the supply for cuticular transpiration reaches the surface of the leaf mainly in this way. Notwithstanding the extreme impermeability of the cuticle, the large area which it exposes relatively to the stomatic openings certainly contributes a sensible proportion of the transpired water, and it seems probable that careful observations on the influence of the speed of an air current on the rate of loss of water may enable us to more sharply differentiate the two forms of transpiration which have hitherto been determined only by comparisons of stomatiferous and non-stomatiferous surfaces.

Sufficient has been said above to indicate the complexity of the problem with which we have to deal, and with all the constantly varying factors acting and reacting on each other, it may well be understood that under natural open-air conditions the thermal relations of a leaf to its surroundings must be constantly undergoing re-adjustment, and that the position of the point of "static thermal equilibrium" must change from moment to moment with every passing cloud, with every gust of wind, and with each change in inclination of the plane of the leaf-lamina to the incident radiation.‡

In the absence of means for instantaneously determining all these factors it is manifestly impossible to ascertain the conditions at any particular moment of time, and there would, perhaps, be no great advantage in doing so even if it were possible. It is the *average* values of the varying factors,

\* It is quite possible that, quite apart from the question of diffusion-phenomena, the irregular action of a strong wind on leaves may result in a certain amount of intermittent compression of the leaf-lamina which may produce tidal ebbs and flows of air through the stomata.

† 'Instit. Bot. Univer. Pavia,' vol. 7, 1902.

‡ The intensity of the radiation received on unit-area varies with the sine of the angle of incidence.

extending over a given interval of time, say a few hours, which it is more important to know, and from these it is possible to deduce a mean expression for the general equation  $Ra = (W + w) + r$ , and for the temperature difference  $\theta - \theta_n$ , or  $\theta_n - \theta$ .

We have recorded in the sequel our endeavours to carry out this idea, but the detailed results will be rendered more intelligible by a preliminary discussion of a few typical examples which illustrate the principles enunciated in the present section of the paper.

Simultaneous experiments were made on two similar leaves of *Helianthus annuus* for the purpose of determining (1) the rate of photosynthesis of carbon dioxide in ordinary air; and (2) the amount of water transpired.

The leaves were exposed to intermittent sunshine of somewhat low intensity for about four hours, the total amount of radiation incident upon them being measured by means of the Callendar radiometer placed alongside the leaves.

In (1) the leaf was enclosed in a glazed case through which ordinary air was passed, and the amount of carbon dioxide assimilated was estimated from its determination in the entering and emergent air, the results being corrected to the partial pressure of the carbon dioxide in the outer atmosphere, which in this instance corresponded to 2.71 parts per 10,000 of air.

Leaf (2), for determining the rate of transpiration, was freely exposed to the air, which had an average temperature of  $16^{\circ}9$  C., and an average velocity of 25.7 kilometres per hour. The partial pressure of the water vapour in the air was 9.21 mm. of mercury as determined from the average readings of the wet and dry bulb thermometers. The area of each leaf was, of course, accurately determined.

The results were as follows:—

- |     |  |                  |
|-----|--|------------------|
| (R) | Average total solar radiation falling on the<br>insolated leaves per square centimetre per<br>minute ..... | 0.2569 calories. |
| (A) | Coefficient of absorption of the leaves .....  | 0.686            |

The actual amount of solar energy intercepted was therefore

$$Ra = 0.2569 \times 0.686 = 0.1762 \text{ calorie per square centimetre per minute.}$$

The amount of carbon dioxide assimilated, reduced to free air conditions, was 2.134 c.c. per square decimetre per hour, or 0.000355 c.c. per square centimetre per minute, which corresponds to an absorption of  $0.000355 \times 5.02 = 0.0017$  calorie per square centimetre per minute ( $w$ ).

The water transpired from the leaf under free air conditions amounted to 1.259 grammes per square decimetre per hour, or 0.000209 gramme per square centimetre per minute. The amount of internal work of vaporization,  $W$ , is therefore  $0.000209 \times 592.6 = 0.1243$  calorie per square centimetre per minute.

The total amount of internal work  $W + w$  performed by the leaf is therefore equivalent to  $0.1243 + 0.0017 = 0.1260$  calorie per square centimetre of leaf-lamina per minute.

In this instance  $Ra$ , the solar radiation absorbed by the leaf, exceeds  $W + w$ , the sum of the internal work of the leaf, by  $0.1762 - 0.1260 = 0.0502$ , which represents the value of  $r$  in calories in the equation

$$Ra = (W + w) + r.$$

This value for  $r$  of 0.0502 calorie per square centimetre per minute represents the *only part of the solar radiation which can have had any heating effect on the leaf*. From the value of  $r$  we can determine the mean temperature-difference between the exposed leaf and its surroundings  $\theta_n - \theta$ , if we know the thermal emissivity of the leaf, for  $\theta_n - \theta = r/2e$ .

The thermal emissivity of a leaf of this nature, for "still air" conditions, is approximately 0.015 calorie per square centimetre of leaf *surface* per minute for a temperature excess of  $1^\circ$ , and the emissivity increases by 0.00017 calorie per square centimetre per minute for an increased air speed of 1 metre per minute. Hence, since the average velocity of the wind in this case was 25.7 kilometres per hour, or 428 metres per minute, the corrected "emissivity" becomes  $0.0150 + 0.00017 \times 428 = 0.0577$  calorie per square centimetre of *surface* per minute for a temperature excess of  $1^\circ$ . Hence the temperature excess of the leaf-lamina above its surroundings will be

$$\theta_n - \theta = \frac{r}{2e} = \frac{0.0502}{0.1154} = 0.43^\circ \text{ C.}$$

Since the average temperature of the air during the experiment was  $16.9^\circ \text{ C.}$ , that of the leaf was about  $17.3^\circ \text{ C.}$

We are now in a position to state with a fair approach to accuracy the manner in which the leaf has disposed of the energy incident upon it, and to obtain some idea of the "economic coefficient" of the leaf under these average conditions. If we denote  $R$ , the total energy incident on unit-area of the leaf in unit-time, by 100, then the disposal of this radiation will be accounted for in the following manner:—

( <i>w</i> ).	Energy used for photosynthesis .....	0·66
( <i>W</i> ).	„ transpiration .....	48·39
		<hr/>
( <i>W</i> + <i>w</i> ).	Total energy expended in internal work .....	49·05
<i>R</i> - <i>Ra</i> .	Solar radiant energy transmitted by leaf ...	31·40
( <i>r</i> ).	Energy lost by “thermal emission” .....	19·55
		<hr/>
		100·00

The “economic coefficient” of the leaf in the above instance was 49·05 per cent. if we include the *whole* of the internal work done in the leaf. If, on the other hand, as is more convenient, we only take into account the *photosynthetic work* on which the plant relies for the production of new formative material, then the “economic coefficient” was only 0·66 per cent.\*

We will now consider a case in which the facilities for the performance of the internal work of vaporization, such as are afforded by fully open stomata, and high temperature and low humidity of the surrounding air, are more than sufficient to utilise the whole of the direct solar radiation absorbed by the leaf. Under these conditions (*W* + *w*) will exceed *Ra*, and the balance of energy required for the internal work will be derived from the environment, the temperature of the leaf falling below that of its surroundings.

The following experiment on leaves of *Helianthus annuus* on a warm dry day in July serves to illustrate the point. The transpiring leaf was placed under the revolving sectors so arranged as to cut off exactly one-half of the total solar radiation which would otherwise have fallen upon it.

<i>R</i> .	Total direct solar radiation falling on the leaf per square centimetre per minute ..	0·2746	calorie.
<i>Ra</i> .	Solar radiation absorbed per square centimetre per minute (coefficient of absorption = 0·686) .....	0·1884	„
<i>w</i> .	Energy expended in assimilation .....	0·0033	„
<i>W</i> .	„ „ transpiration .....	0·3668	„
<i>W</i> + <i>w</i> .	Total energy used for internal work .....	0·3701	„

Hence the energy (*r*) which the leaf has derived from its surroundings = (*W* + *w*) - *Ra* = 0·1817 calorie per square centimetre of leaf-lamina per minute.

Notwithstanding the fact that the leaf was receiving an incidence of solar radiation equivalent to 0·2746 calorie per square centimetre per minute, its

\* In this restricted sense the “economic coefficient” of the leaf is the ratio of the energy utilised by photosynthesis to the total radiation falling on the leaf.



temperature must in this case have been *lower* than that of its surroundings, and this temperature difference  $\theta - \theta_n$  will again be measured by  $r/2e$ .

Since the average velocity of the wind during the experiment was 12.0 kilometres per hour (= 200 metres per minute) and the "emissivity" of the leaf under "still air" conditions was 0.015 calorie per square centimetre of surface per minute for a temperature difference of  $1^\circ$ , the "emissivity,"  $e$  for the above speed of the air is represented by  $0.015 + 200 \times 0.00017 = 0.0490$ , hence,

$$\theta - \theta_n = 0.1817 \div (2 \times 0.049) = 1.84^\circ \text{ C.}$$

The mean temperature of the surrounding air being  $27.2^\circ \text{ C.}$ , that of the leaf was consequently  $27.2 - 1.84 = 25.36$ .

If, in this last experiment, we represent the sum of the energy received by the leaf both from solar radiation and from its surroundings by 100 we get the following results:—

(w).	Energy used for photosynthesis .....	0.72	calorie.
(W).	„ transpiration.....	80.38	„
		<hr/>	
(W + w).	Total energy expended in internal work...	81.10	„
R - Ra.	Solar radiant energy transmitted by leaf..	18.90	„
		<hr/>	
		100.0	„

Since the receipt and expenditure of energy must necessarily balance each other for a given period of time it is somewhat instructive to arrange the results in the form of a "Revenue and Expenditure Account" for the leaf. For the last mentioned experiment this comes out as follows:—

	Calories per square centimetre of leaf-lamina per minute.
<i>Revenue account—</i>	
Total solar radiation incident on the leaf .....	0.2746
Gain of energy from surroundings .....	0.1817
<hr/>	
Total energy reaching 1 sq. cm. of leaf per min. ...	0.4563
<i>Expenditure account—</i>	
Energy used up in photosynthesis .....	0.0033
„ transpiration .....	0.3668
<hr/>	
Total energy used for internal work.....	0.3701
Incident solar energy transmitted .....	0.0862
<hr/>	
	0.4563

When a leaf is exposed to full sunshine the radiant energy which is utilised for the photosynthetic process represents only a very small part of the total incident radiation. If we restrict the term "economic coefficient" to the ratio of these two values, the full radiation falling on the leaf being taken as 100, it is evident that the leaf is an extremely wasteful transformer of energy, since it receives a very large amount of superfluous energy which does not contribute to the main function of the leaf, and has to be dissipated by some means.

If for the purpose of argument we assume that photosynthetic work is confined to that portion of the solar spectrum corresponding to the principal absorption-band of chlorophyll, lying between the lines B and C, some idea may be obtained of the maximal theoretical efficiency of a leaf exposed under the most favourable conditions to full sunshine, provided we know the relation of the energy in this restricted portion of the spectrum to the total energy.

The question has already been discussed by one of us from this point of view,\* and the conclusion was reached that the maximal "economic coefficient" *for full sunshine* would probably be about 6·5 per cent. if the leaf were in a position to sift out and utilise the whole of the particular grade of energy useful for photosynthetic work. But this implies a set of conditions which can never exist in nature owing to the limits imposed on the assimilatory process by the high state of dilution of the "atmospheric carbon dioxide."

That the photosynthetic rays, even in sunlight of very moderate intensity, are in excess of the power of the leaf to utilise them has been shown by the experiments described in Part II, p. 54, in the first place by the increased assimilatory effect produced under constant or practically constant illumination by increasing the carbon dioxide in the surrounding air, and secondly by observing the rate of photosynthesis in air of fixed carbon dioxide-content when the leaf is submitted to solar radiation of varying and known relative intensity.

It was found, for instance, when solar radiation of an average intensity of about 0·5 calorie per square centimetre per minute was reduced to about one-third of this intensity by passing through a thin canvas screen, forming an artificial "cloud," that it still contained an excess of photosynthetic rays over and above what was necessary to produce maximal assimilation in ordinary air; for by means of the revolving-sector-method the intensity of the radiation could be still further reduced to one-quarter, that is to say, to one-twelfth of the original amount, before there was any sensible diminution in the assimilatory power of a leaf submitted to its influence.†

\* See 'Pres. Address,' section B, 'Brit. Assoc. Rep.,' 1899, p. 681.

† In passing it may be noted that the ratio which the photosynthetic radiation bears to the total

This excess of photosynthetic radiation in weakened sunlight is a fact of the highest importance to the plant, since it enables the leaf to carry out unimpaired the main function of assimilation in diffuse light, and in sunlight of a considerable degree of obliquity.\* It has also an important bearing on the "economic coefficient" of the leaf, for it is manifest that this must vary very much according to the intensity of insolation. The "coefficient" will be at a maximum when the insolation is just sufficient to produce the maximal rate of assimilation for a given partial pressure of carbon dioxide in the air, and will decrease with increased incident radiation. The accuracy of this deduction is shown by the detailed results which follow, especially those obtained by experiments with revolving sectors.

A few words still remain to be said about the dissipation of the superfluous energy absorbed by the leaf. We have already seen that this is brought about by the two processes of water vaporisation (transpiration) and thermal emission. The relative part taken by each of these processes will vary greatly according to the nature of the plant and the surrounding conditions. In the case of plants well adapted to water-conduction and provided with abundant stomata, the transpiratory "safety-valve" no doubt plays the more important part, and the temperature-gradient between the leaf and its environment need never be large in non-saturated air. For instance, in the case of a leaf transpiring at the moderate rate of 500 grammes per square metre per hour, it can readily be shown that the vaporisation of this amount of water will absorb about 0·5 calorie per square centimetre per minute. We have never observed a higher maximal value for solar radiation at Kew than about 1·0 calorie per square centimetre per minute, and for observations extending over several hours it has seldom exceeded 0·5 calorie.

solar radiation ought to be approximately determinable by the use of the revolving radial sectors described in Part II, p. 54.

In the particular case cited above no effect on assimilation was produced until the solar radiation of 0·5 calorie per square centimetre per minute had been reduced by the screening to one-twelfth of its original value, *i.e.*, to 0·041 calorie. The observed rate of assimilation at this point was 2·07 c.c. of carbon dioxide per square decimetre per hour, or 0·00034 c.c. per square centimetre per minute, which must mark the stage at which practically the whole of the rays capable of producing photosynthesis were utilised for that purpose. From what has been said before it follows that this amount of assimilated CO<sub>2</sub> corresponds to an absorption of energy of  $0·00034 \times 5·02 = 0·0017$  calorie per square centimetre per minute. Since no selective absorption has taken place in the screening process, the proportion of photosynthetic rays in the reduced radiation falling on the leaf, *i.e.*,  $\frac{0·0017 \times 100}{0·041} = 4·1$  per cent., also represents the percentage of photosynthesizing energy in the original unscreened solar radiation.

\* It follows that the limiting factor in assimilation in ordinary sunlight of even a low degree of intensity is the high degree of dilution of the atmospheric carbon dioxide.

Where transpiration is at a minimum, especially in the extreme case of xerophytic plants, the dissipation of the absorbed radiant energy by *thermal emission* becomes all important, and we are now able for the first time to apply certain numerical values to the dissipation of energy from this cause, which are of some interest.

Since the emissivity of a leaf surface approximates to 0.015 calorie per square centimetre of surface for a temperature excess of 1°, a rise in temperature of the leaf of only 10° will, even under *still air* conditions, give a dissipation of energy equivalent to  $10 \times 2 \times 0.015 = 0.3$  calorie per square centimetre per minute, and in a gentle breeze of only 10 kilometres per hour, this emission will be increased to 0.864 calorie per square centimetre per minute. Hence in the thermal emissivity of a plant we have a vary potent factor for keeping down the temperature, even in the absence of transpiration.

Hitherto we have been regarding only those cases in which the incidence of solar radiation is *normal* to the leaf surface, conditions which seldom occur in nature, especially when radiation is powerful, as in the tropics or at high altitudes, where the self-adjusting mechanism of the plant, and its habit, are such as seldom to allow the leaf to be placed in a position favourable for receiving the full solar radiation.\*

Since the intensity of the radiation received on unit-area *varies with the sine of the angle of incidence*, a radiation equal to 1 calorie per square centimetre per minute will be reduced to 0.707 calorie at an obliquity of 45°, and to 0.5 calorie, or one-half of its normal intensity, at an obliquity of 30°.†

#### Section (2).—*Experimental.*

##### (a) *Determination of R, the total incident Radiation.*

The total solar radiant energy incident on a leaf in a given time is very conveniently measured by the Callendar's radiometer and recorder already referred to in Part I (see p. 39). This instrument is particularly well adapted to experiments of this kind, since it receives and records the sky-radiation as well as that of direct sunlight, and the area covered by the receiving coils of the differential thermometer is comparable in magnitude with the areas of the

\* On this point cf. A. J. Ewart on the "Effects of Tropical Insolation" ('Annals of Bot.', vol. 11, p. 439), who states from observation that "no tropical plant places or allows its leaves to be in such a position that the upper surfaces are at right angles to the sun's incident rays when at the zenith."

† With increasing obliquity there will also be less penetration of the radiations owing to increased reflection. In the case of light, whilst the reflection from the surface of glass is about 2.5 per cent. for normal incidence, it is 3.4 per cent. for an obliquity of 50°, and as much as 29.9 per cent. at an obliquity of 15°.

leaves employed. Instruments of the type of the Ångström's compensating pyrhelimeter, in which the radiation is received through narrow slits or diaphragms, to the almost complete exclusion of sky-radiation, are not so suitable for investigation of this nature.

The radiometer was always exposed in close juxtaposition to the leaf, and in the same plane as the leaf-lamina, so as to ensure equality in the amount of energy received by the two surfaces.

At the conclusion of an experiment, the integrated record, as given by the planimeter reading, was reduced to *water-gramme-units of energy (calories) incident on one square centimetre per minute*.

As examples of some of the highest readings which we have obtained in this way in full sunshine, we may give the following:—

Table I.

Date.	Time.	Solar radiation in calories per square centimetre per minute.
July 10, 1900 .....	4.0 P.M.	0.972
" 17, " .....	12.20 "	1.019
June 27, 1901.....	12.10 "	0.934
" 27, " .....	2.20 "	0.941
July 20, " .....	12.20 "	0.932

The observations above were made on exceptionally clear days, and with the sun's rays normal to the receiving instrument. The values are somewhat

Table II.

Date.	Duration of observation in hours.	Percentage of sunshine.	Mean solar radiation in calories per square centimetre per minute.
June 25, 1901.....	4.30	46	0.246
July 9, " .....	2.54	100	0.479
" 11, " .....	1.93	100	0.549
" 15, " .....	0.90	70	0.393
" 17, " .....	2.59	76	0.499
" 18, " .....	1.55	100	0.550
" 19, " .....	1.26	75	0.533

low, a result which is no doubt due to the low-lying position of Kew Gardens and to the absorptive influence of the attenuated veil of London smoke in the lower regions of the air.

When observations are extended over several hours, the mean result, even on the clearest day, seldom exceeded about 0.550 calorie per square centimetre per minute, as is shown by Table II.

The column headed "percentage of sunshine" gives the proportion of the total time occupied by the experiment, during which the sunshine was of sufficient intensity to produce a record on the Campbell-Stokes' burning recorder of the Kew Observatory.

(b) *The Absorption of Solar Radiation by the Leaf-lamina: Determination of  $a$ , the "coefficient of absorption" of the leaf.*

As a necessary preliminary to the discussion of the quantitative relations between the energy incident on the leaf and the internal work produced, we must determine the respective proportions of the radiant energy of sunlight which are transmitted and absorbed by the leaf-lamina.

This *coefficient of absorption*, a value which we have denoted by  $a$  in the general thermal equations of the leaf referred to in Section (1), was determined in the following manner:—

Over the glass cover of the Callendar's radiometer was fixed a closely-fitting cardboard-cover, out of which a square opening was cut of a sufficient size to expose the platinum-spirals, the opening being bisected by the division between the spirals. The leaf under experiment, with its petiole dipping into a small tube of water, was then laid down on the cover of the radiometer in such a manner that the mid-rib\* lay between the spirals and the leaf-lamina was symmetrically disposed over the coils. Over the leaf there was then placed another piece of cardboard with a similar square opening, and when this was tied down to the radiometer the lamina was in the right position.

A favourable day of bright sunshine was selected for the experiment, when we could rely on the solar radiation remaining constant, or nearly so, during the few minutes required for an observation.

The plan adopted was in the first place to obtain a measure of the unobstructed solar radiation falling normally on the platinum-spirals, waiting until the pen of the recorder drew a straight line on the drum. Another similar observation was then made after the interposition of the leaf-lamina,

\* To facilitate the leaf being brought into close apposition to the glass cover of the radiometer, slits were cut in opposite sides of the cardboard frame in order to receive the mid-rib.

and finally a second observation of the unobstructed radiation. The effect produced by the leaf was referred to the mean of the first and third observations with full radiation, and the result was expressed in the form of a *coefficient of absorption* ( $a$ ) for the leaf-lamina, the full radiation falling on the leaf being taken as unity.

The only sensible error to which this method is liable is that due to *reflection* of radiation from the leaf-surface, an error which would tend to unduly increase the estimated coefficient of absorption. With the perpendicular incidence of sunlight such as was generally employed in these experiments the amount of reflection must, however, have been very small.

The estimation of the coefficient of absorption cannot be perceptibly influenced by re-radiation from the leaf to the platinum-spirals, since, in the first place, during the very short time the experiment lasts, the rise of temperature of the lamina will be very small, especially as transpiration is going on; and, secondly, the glass cover of the radiometer is very opaque to the obscure radiation which the leaf would emit.

With the same leaf and at different times of the day the method gives very concordant results, as will be seen from the following obtained with a leaf of *Helianthus annuus*. In these experiments the actual values of the unobstructed solar radiation (R) varied from 0.591 to 0.636 calorie per square centimetre per minute.

		Coefficient of absorption for sunlight.
<i>Helianthus annuus</i> (1).....		0.687
"      "      (2).....		0.689
"      "      (3).....		0.684

Although the coefficient of absorption is fairly constant for mature and healthy leaves of the same species of plant it shows considerable variation in the leaves of different species, as will be seen from the following Table III, in which are given the mean values for a number of different plants. The values of the *coefficients of transmission* (i.e.,  $1-a$ ) are also given in this instance.

A series of observations was now undertaken in order to determine how far individual leaves of the same plant differ in their coefficient of absorption for solar energy, and in order to bring out any possible correlation which may exist between this property and the age of the leaf, the experiments were carried out on leaves taken from the plant in the *serial order of their development*.

Table III.—Coefficients of Absorption and Transmission of the Radiant Energy of Sunlight for Leaves of Different Plants.

Plant.	Coefficient of absorption ( $a$ ).	Coefficient of transmission ( $1 - a$ ).
<i>Helianthus annuus</i> .....	0·686	0·314
<i>Polygonum Weyrichii</i> .....	0·647	0·353
„ <i>Sachalinense</i> .....	0·691	0·309
<i>Petasites officinalis</i> .....	0·728	0·272
<i>Silphium terebrinthaceum</i> .....	0·699	0·391
<i>Arctium majus</i> .....	0·728	0·272
<i>Verbascum olympicum</i> .....	0·758	0·242
<i>Senecio grandifolius</i> .....	0·774	0·226

The following table gives the results of two different series of observations of this kind made on leaves of *Senecio grandifolius* :—

Table IV.—Coefficient of Absorption of the Radiant Energy of Sunlight for Leaves of *Senecio grandifolius* taken from the same Plant in Serial Order.

	Series A. Coefficient of absorption.	Series B. Coefficient of absorption.
Leaf 1 (youngest mature leaf)	0·750	0·776
„ 2 .....	0·748	0·771
„ 3 .....	0·757	0·763
„ 4 .....	0·762	0·784
„ 5 .....	0·793	0·776
„ 6 .....	0·778	—

It will be seen that the variations in the values of the coefficient of absorption in this plant are not large, and that such as they are they show little or no relation to the age of the leaf.

In another similar series of experiments with *Polygonum Sachalinense*, recorded in the following table, there was some indication of a slight increase of the coefficient of absorption with the age of the leaf.



Table V.—Coefficient of Absorption of the Radiant Energy of Sunlight for Leaves of *Polygonum Sachalinense* taken from the Plant in Serial Order.

	Coefficient of absorption.
Leaf 1 (youngest) .....	0·687
„ 2 .....	0·681
„ 3 .....	0·696
„ 4 .....	0·702

(c) *The Selective Absorption of Radiant Energy by the Leaf.*

In considering the general thermostatic and thermodynamic problems arising out of the reception and utilization of radiant energy by the leaf, we have so far only been concerned with the gross amount of energy received, irrespective of its particular grade. As long as we confine ourselves to the consideration of *single* leaves the principles which have hitherto guided us are sufficient to determine the thermal relations of a leaf to its environment without reference to the particular quality of the rays transmitted or absorbed by the leaf-lamina. On the other hand, any attempt to determine the thermal and other effects induced by sunlight which has already been filtered through one or more leaves must necessarily take into account the property of *selective absorption* possessed by the lamina, a property which is mainly due to the colouring matter of the leaf.

If the leaf-lamina absorbed equal proportions of the various undulations incident upon it in the form of solar radiation, that is to say, if it possessed no power of selective absorption, we should expect the transmitted portion of the radiation to diminish in geometric proportion as the number of similar leaves was increased in arithmetic proportion. Thus, taking the incident radiation as unity, and assuming that we have a leaf with a coefficient of absorption of 0·687, and therefore a coefficient of transmission of 0·313, if selective absorption does not come into play we ought to obtain a transmission through *two* superimposed and similar leaves of  $0·313^2 = 0·098$ , with *three* such leaves of  $0·313^3 = 0·030$ , and with *n* leaves a transmission of  $0·313^n$ .

In a green leaf, however, we have to deal with a screen which is eminently selective in its absorbing power, a fact which is clearly brought out by the results given in the following table, which show the increased transmission by a second and third leaf of the heat rays which have passed through the first. The experiments were made with the Callendar's radiometer by the successive superposition of the leaves.

Table VI.—Proportion of the Radiant Energy of Bright Sunshine Absorbed and Transmitted by the Successive Superposition of Three Leaves.

Full unscreened radiation = 100.

Name of plant.	Radiation absorbed. Per cent. of total.	Radiation transmitted. Per cent. of total.	Radiation which would have been transmitted in absence of selective absorption.
Series A. <i>Polygonum Weyrichii</i> , coefficient of absorption, 0·647—			
One leaf .....	64·7	35·3	—
Two leaves .....	80·8	19·2	12·4
Three leaves .....	84·5	15·5	4·4
Series B. <i>Helianthus annuus</i> , coefficient of absorption, 0·687—			
One leaf .....	68·7	31·3	—
Two leaves .....	82·6	17·4	9·7
Three leaves .....	88·4	11·6	3·0

The selective absorption of solar radiation by the green colouring matter of leaves, also comes out very clearly in certain experiments described by Timiriazeff, and referred to further on. He found, for example, that whilst the chlorophyll which had been dissolved out of a given area of a Maple leaf arrested 27 per cent. of the energy of direct sunlight, this absorption was only increased to 31 per cent. by a triple concentration of the solution.

(d) *Relative absorption of Solar Radiation by Albino and Green leaves of the same plant.*

The plant selected for these experiments was *Negundo aceroides*, and since the leaves were too small to be used with the Callendar's radiometer in the manner already described, other means had to be devised for determining the coefficient of absorption of the leaf. The experiments were kindly undertaken by Dr. W. E. Wilson, and were carried out during the past summer at his Observatory at Daramona, Westmeath.

In the first instance an attempt was made to employ the Boys' radiometer, by reflecting a portion of the sun's image from a heliostat on to the suspended thermo-electric junction, and taking successive readings of the galvanometer with and without the interposition of the leaf-lamina. It was

found, however, that under these conditions both the white and the green leaves acted as perfect screens, and completely prevented any sensible amount of solar radiation from reaching the sensitive part of the instrument.

The same difficulty was also experienced in attempting to adapt the Angström's pyrheliometer to the purpose, the failure in both cases being due to the fact that the absorbing leaf-lamina, which must necessarily be at some little distance from the sensitive thermo-electric junction, so far scatters the radiation which passes through the small apertures of the instruments, that the vertical component of the transmitted rays, which can alone affect the instrument, becomes very small. The aperture covered by the leaf becomes, in fact, a new focus of radiation which spreads the rays over an area much larger than that occupied by the receiving surface of the sensitive portion of the instrument.

It is necessary, therefore, that the receiving surface forming the thermometer should have, as in the Callendar's instrument, a considerable extension, and should be well overlapped by the leaf, which must admit of being brought close to the receiving surface.

For leaves too small for the Callendar's radiometer, a Rubens' thermopile was found to be suitable, the leaf being placed between two plates of thin glass and brought within about a millimetre of the receiving end of the pile. The absorptivity of the leaf for bright sunshine was determined by observing the amount of radiation transmitted through the glass plates, both with and without the interposition of the leaf.

A series of concordant experiments made in this manner with the white and green portions of a leaf of *Negundo*, gave the following mean results in bright sunshine:—

	Transmission.	
Through glass alone.....	100·0	*
White leaf interposed .....	25·5	
Green „ „ .....	21·3	

These results lead to the following values for the coefficients of absorption and transmission for the white and green portions of the leaf respectively.

Table VII.—Absorption and Transmission of the Radiant Energy of Sunlight by the White and Green portions of the Leaf of *Negundo aceroides*.

	Coefficient of absorption.	Coefficient of transmission.
White leaf lamina .....	0·745	0·255
Green „ „ .....	0·787	0·213

If the transmission through the albino-leaf is taken as 100, that of the green leaf will be represented by 83·5, a difference of 16·5 per cent., which may be regarded as expressing the increase in the absorptive power due to the colouring matters of the leaf.

In connection with the increased absorption induced by the leaf-chlorophyll, it is of interest to compare the above results with those of Timiriazeff, which were obtained by a totally different method.\*

Timiriazeff's mode of procedure was to punch out of a leaf a circular piece of known area, and to dissolve its green colouring matter in a volume of alcohol just sufficient to fill a glass cell of exactly the same cross-section as the area of the leaf. The absorptive power of the coloured solution for the radiant energy of sunshine was then determined by means of a delicate thermopile, the absorption for the glass and solvent being ascertained separately. The difference between the two readings was taken as representing the absorption due to the chlorophyll.

Timiriazeff obtained by this method the following results for the absorption induced by the chlorophyll of single leaves.

	Absorption of direct sunlight.
Maple .....	27·0 per cent.
Lime .....	29·0 „
Oak... ..	23·5 „
Plantain .....	23·4 „
Potamogeton .....	20·0 „

The leaf of the *Negundo* was not included in Timiriazeff's experiments, but a consideration of his results points to the probability of this leaf showing by his method a chlorophyll-absorption of more than the 16·5 per cent., which was the amount we found by direct observations on the leaf-lamina.

The widely different methods of experiment would account for this, since the chlorophyll when in solution is under more favourable conditions for exerting its maximum absorptive power than it is under the natural conditions which exist in the living leaf. In the latter case, owing to the particulate nature and scattered distribution of the chlorophyll-bodies, the transmitted radiation must be subjected to a less complete selective absorption than when the chlorophyll is in a state of solution.

\* See Croonian Lecture, 'Roy. Soc. Proc.,' 1903, p. 449.

(e) *The Determination of the Thermal Emissivity ( $e$ ) of the Leaf-lamina.*

For a full consideration of the experimental methods adopted for a determination of the thermal emissivity of a leaf-lamina reference must be made to a separate communication on the subject.\*

The mean value of the emissivity for the four kinds of leaf examined was for, "still air" conditions, 0.0145 calorie per square centimetre of leaf surface per minute for a temperature excess of 1° C. In moving air the emissivity increases by 0.000172 calorie per square centimetre per minute for every metre per minute increase in the velocity of the air moving over the surface of the leaf-lamina.

(f) *Details of Experiments on Leaves submitted to Solar Radiation of known Intensity, showing the mode of Disposal of the Incident Energy under Defined Conditions.*

The data of these experiments have been brought together in Tables VIII, IX, X, and XI. Their general arrangement will be understood from what has been said in Section (1) Part III on the thermal relations of a leaf to its surroundings, but some detailed explanation of the headings of the columns is desirable at this point.

Tables VIII and IX contain the results of a number of experiments on leaves of different species of plants submitted to solar radiation of known intensity, whilst a direct determination was made of the internal work of photosynthesis and of transpiration.

In order that the assimilatory experiments should be carried on under favourable conditions of temperature, the full solar radiation was, in most cases, modified by passing it through a thin canvas screen before it reached the leaf.

In Table VIII Columns (1) and (2) require no comment.

Column (3) headed "percentage of sunshine," indicates the proportion of the time occupied by the experiment, during which the unobstructed solar radiation was sufficiently intense to be recorded on the Campbell-Stokes burning recorder.

Column (6) gives the average partial pressure of the water-vapour in the air as deduced from the reading of the wet and dry bulb thermometers as given in Columns (4) and (5).

Column (7) gives the average humidity of the air when that of saturated air = 100.

\* See Brown and Wilson, *infra*, p. 122.

Column (8) gives the average velocity of the wind during the experiment in kilometres per hour.

Column (9) headed "difference of temperature between leaf and air" requires some explanation. The values are deduced, in the first place, from the difference between  $Ra$ , the energy absorbed by the leaf, and  $W + w$ , the energy used up in the internal work; and, secondly, from the known *thermal emissivity* of the leaf in an air-current of the mean velocity of the wind during the experiment. If the emissivity of the leaf per square centimetre per minute for a temperature-excess of  $1^\circ$  be represented by  $e$ , then the temperature difference between the leaf and the surrounding air will be represented by  $\frac{Ra - (W + w)}{2e}$ . If  $Ra$  exceeds  $W + w$  the temperature of the leaf will be *above* that of its surroundings, whereas if  $Ra$  is less than  $W + w$  the leaf temperature will be the lower.

The values of Column (10), headed "estimated temperature of the leaf," were obtained from the dry bulb temperatures by adding or subtracting the values of Column (9).

Column (11) gives the excess of the partial pressure of the water-vapour in the air-spaces of the experimental leaf over that of the outside atmosphere. It is, in fact, the differential partial pressure, measured in millimetres of mercury, between the point of saturation corresponding to the leaf temperature as given in Column (10) and the partial pressure of the water-vapour of the outer air as given in Column (6). It is a measure of the "diffusion-gradient" of the water-vapour existing between the interspaces of the leaf and the external air. Assuming all other conditions to be identical the rate of transpiration should be proportional to the values given in this column.

Column (12) gives the rate of photosynthesis determined directly in the manner already fully described. The results are given in terms of cubic centimetres of atmospheric carbon dioxide utilised by one square decimetre of the leaf in one hour.

Column (13) gives the rate of transpiration as directly determined, the results being expressed in grammes of water transpired by one square decimetre of leaf-lamina in one hour.

Columns (14) to (21) include the results obtained by means of the Callendar's radiometer and give an account of the manner in which the incident radiation has been utilized by the leaf. The values are here given in terms of water-gramme-units (calories) per square centimetre of leaf-lamina per minute.

Column (14) gives a measure of the total solar radiation incident on the leaf, a value which has been denoted by  $R$  in the general thermal equations.

Column (15) gives the coefficient of absorption of the leaf for solar radiation, this coefficient being denoted by  $a$ .

Column (16) gives the proportion of incident solar radiation which is absorbed by the leaf, and which must manifestly be equivalent to the incident radiation multiplied by the coefficient of absorption, *i.e.*, to  $Ra$ .

The amount of energy *transmitted* through the leaf will, of course, be represented by  $R - Ra$ .

Column (17) gives the amount of energy used up by the endothermic process of photosynthesis.

As already explained in Section (1) Part III (p. 77), these values are deducible from the volume or mass of carbon dioxide assimilated by the leaf as given in Column (12). The volume of carbon dioxide assimilated per square centimetre of leaf-lamina per minute, when multiplied by 5.02, gives a measure of the energy  $w$  used up in photosynthesis, expressed in calories for the same unit-area and unit-time.

Column (18) in the same manner gives a measure of the amount of energy,  $W$ , expended in the vaporization of water by the leaf. The values are deduced from the experimental results of Column (13), giving the water transpired from a given area of leaf in a given time.

The numbers are obtained by multiplying the grammes of water transpired by one square centimetre of the leaf-lamina per minute by the value for the latent heat of water, which at  $20^\circ$  is 592.6 calories.

Column (19) gives a measure of the expenditure of energy for the total internal work of the leaf, both for protosynthesis and water vaporization—*i.e.*,  $W + w$ . The values given are the sum of those of Columns (17) and (18).

Column (20) gives the actual amount of energy lost per unit-area of leaf-lamina and unit-time owing to re-radiation and the conductive and convective properties of the surrounding air. This is the difference between  $Ra$  and  $W + w$ , when  $Ra$  is the greater. It is the only portion of the incident radiation which can produce any rise of temperature in the leaf.

When  $Ra$ , the incident radiation falling on the leaf and absorbed by it, is less than  $W + w$ , the energy used up in internal work, it is manifest that the leaf must draw upon its surroundings for the balance. Where this condition of things exists it is recorded in Column (21). The leaf is then *lower* in temperature than its surroundings.

The results tabulated in Columns (14) to (21) of Table VIII, giving the actual loss and gain of energy by the insolated leaf per square centimetre per

Table VIII.—First Series of Experiments on Leaves under Varying the Leaves and

(1)	Species of plant and general conditions of experiment.	Meteorological data.						Difference of temperature between leaf and air, °C.
		Percentage of sunshine recorded.	Dry bulb thermometer.	Wet bulb thermometer.	Partial pressure of water-vapour in air in millimetres of mercury.	Degree of humidity of air. Saturated air = 100.	Velocity of wind in kilometres per hour.	
I. June 29, 1900	<i>Polygonum Weyrichii</i> — Intermittent sunlight without any screen. Duration of experiment, 4·75 hours	72	20·5	16·5	9·09	69	24·4	+1·98
II. June 19, 1900	<i>Polygonum Weyrichii</i> — Leaves exposed to full sunshine under thin canvas screen. Duration of experiment, 5 hours	80	21·1	14·8	8·87	47	26·5	+0·10
III. June 22, 1900	<i>Polygonum Weyrichii</i> — Intermittent sunlight. Leaves under thin canvas screen. Duration of experiment, 4·2 hours	56	18·3	12·7	8·13	51	25·7	+0·05
IV. July 3, 1900	<i>Polygonum Weyrichii</i> — Intermittent sunshine with some showers. Leaves under canvas screen. Duration of experiment, 4·3 hours	42	16·8	13·8	9·98	70	10·6	+0·44
V. July 11, 1900	<i>Polygonum Weyrichii</i> — A hot cloudless day. Leaves exposed under canvas screen. Duration of experiment, 4·9 hours	100	27·2	19·6	12·33	44	26·5	+0·15
VI. Sept. 4, 1900	<i>Tropæolum majus</i> — Diffused light with very little sunshine. Leaves exposed under canvas screen. Duration of experiment, 3·3 hours	3·3	17·0	12·7	8·58	60	9·1	+0·58
VII. Sept. 7, 1900	<i>Tropæolum majus</i> — Leaves in sunlight under canvas screen. Duration of experiment, 5 hours	55	20·1	14·7	9·49	53	5·4	+1·27



Conditions of Insolation, Illustrating the Thermal Interchanges between their Surroundings.

(10)	(11)	(12)	(13)	Loss or gain of energy by the leaf in calories per square centimetre of leaf-lamina per minute.							
				R. Solar radiation incident on leaf.	a. Coefficient of absorption.	Ra. Solar radiation absorbed by leaf.	w. Energy expended in assimilation.	W. Energy expended in transpiration.	W + w. Total energy used for internal work.	r. Energy lost by re-radiation and air-convection.	Energy received from surroundings.
22·4	11·02	3·20	0·599	0·6120	0·647	0·3959	0·0026	0·0592	0·0618	0·3341	—
21·2	9·82	3·758	1·054	0·1942	0·647	0·1256	0·0031	0·1041	0·1072	0·0184	—
18·3	7·49	3·058	0·868	0·1503	0·647	0·0972	0·0025	0·0857	0·0882	0·0090	—
17·2	4·59	2·271	0·517	0·1431	0·647	0·0926	0·0019	0·0510	0·0529	0·0397	—
27·3	14·61	1·479	1·291	0·2418	0·647	0·1565	0·0012	0·1275	0·1287	0·0278	—
17·5	6·27	1·498	0·1410	0·0889	0·700	0·0622	0·0012	0·0139	0·0151	0·0471	—
21·3	9·31	2·078	0·2430	0·1461	0·700	0·1022	0·0017	0·0240	0·0257	0·0765	—

Table VIII—

(1)	Species of plant and general conditions of experiment.	Meteorological data.						Difference of temperature between leaf and air, °C.
		Percentage of sunshine recorded.	Dry bulb thermometer.	Wet bulb thermometer.	Partial pressure of water-vapour in air in millimetres of mercury.	Degree of humidity of air. Saturated air = 100.	Velocity of wind in kilometres per hour.	
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
VIII. Sept. 11, 1900	<i>Tropaeolum majus</i> — Leaves in sunlight under canvas screen. Duration of experiment, 4·8 hours	95	17·6	12·2	7·78	55	21·8	+0·49
IX. June 6, 1900	<i>Petasites albus</i> — Leaves in sunlight under canvas screen. Duration of experiment, 3·2 hours	97	21·1	14·4	8·74	46	12·2	+0·96
X. June 26, 1900	<i>Petasites albus</i> — Leaves in weak diffused sunlight under canvas screen. Duration of experiment, 5·3 hours	16	15·5	11·9	8·44	64	25·4	+0·07
XI. July 5, 1900	<i>Petasites albus</i> — Leaf in full sunlight for 4/10 of time; afterwards under canvas screen. Duration of experiment, 5·2 hours	45	19·5	16·6	12·11	71	16·0	+0·54
XII. Aug. 7, 1900	<i>Helianthus annuus</i> — Leaf still attached to plant for assimilation experiment. No screen used. Duration of experiment, 5 hours	50	16·9	13·2	9·21	65	25·7	+0·28
XIII. Aug. 11, 1900	<i>Helianthus annuus</i> — Full solar radiation without any screen. Detached leaves. Duration of experiment, 3·7 hours	87	19·4	14·2	9·24	54	7·4	+1·54

N.B. — In the case of experiments marked thus \* the

*continued.*

Estimated temperature of leaf.				Loss or gain of energy by the leaf in calories per square centimetres of leaf-lamina per minute.							
(10)	Excess of partial pressure of water-vapour in leaf over that of air in millimetres of mercury.	Assimilation in cubic centimetres of CO <sub>2</sub> per square decimetre per hour.	Transpiration in grammes of water per square decimetre per hour.	R. Solar radiation incident on leaf.	a. Coefficient of absorption.	Ra. Solar radiation absorbed by leaf.	w. Energy expended in assimilation.	W. Energy expended in transpiration.	W + w. Total energy used for internal work.	r. Energy lost by re-radiation and air-convection.	Energy received from surroundings.
18·1	7·64	1·210	0·1340	0·1282	0·700	0·0897	0·0010	0·0132	0·0142	0·0755	—
22·0	10·89	2·565	0·3373	0·1802	0·728	0·1311	0·0021	0·0333	0·0354	0·0957	—
15·6	4·73	1·879	0·7119	0·1171	0·728	0·0852	0·0015	0·0703	0·0718	0·0134	—
20·0	5·25	2·507	0·6614	0·1834	0·728	0·1335	0·0021	0·0653	0·0674	0·0661	—
17·1	5·27	2·134	1·259	0·2569	0·686	0·1762	0·0017	0·1243	0·1260	0·0502	—
20·9	9·11	*2·40	3·962	0·7341	0·686	0·5035	0·0020	0·3913	0·3933	0·1102	—

values were estimated, not obtained by direct experiment.

minute, are rearranged in a more convenient form in Table IX, where the total amount of energy received by the leaf-lamina is represented by 100, and is accounted for by the two modes of internal work in the leaf, the energy lost by transmission through the lamina, and that lost by re-radiation and the cooling action of the surrounding air.

The percentage of energy used in photosynthesis,  $w$ , may be regarded as the true "economic coefficient" of the leaf—that is to say, the percentage of the total incident energy which, under the particular conditions of each experiment, the mechanism of the leaf-lamina has been able to transform into useful photosynthetic work contributing to the production of new material for the plant.

The experiments recorded in Tables VIII and IX were carried out on different days on which the insolation and atmospheric conditions varied, so that they are not comparable with each other except in a general way, even where leaves of the same species of plant were employed.

In the second series of experiments, the details of which are given in Tables X and XI, simultaneous duplicate experiments were made on similar leaves for which all the external conditions were the same except the degree of insolation represented by  $R$ . Whilst one leaf, A, was exposed to the full sunshine, the other, B, was exposed behind revolving sectors which cut off a definite proportion of the solar radiation. Thus, as far as regards the conditions which were under control, there was only one variable introduced, that of  $R$ , and the two members of each pair of experiments are therefore capable of being compared with each other from this point of view. It must not, however, be lost sight of that variations in the value of  $R$  tend to introduce secondary effects on the internal work of transpiration, not only by altering the temperature of the leaf, but also indirectly by altering the degree of opening of the stomata. Although, therefore, such experiments as those recorded in Tables X and XI admit, under the controlled conditions of incident radiation, of a much closer comparison than those of Tables VIII and IX, still it is practically impossible to produce conditions under which only one factor at a time shall vary, owing to the mutual dependence of the various factors one on the other, a fact which has already been fully discussed in Section (1), Part III.

The experiments of Series A of Tables X and XI were all carried out under the full available insolation, but, notwithstanding this fact, it will be noted that the condition of the stomata and the excess of partial pressure of water-vapour between the interspaces of the leaf and the surrounding air were so favourable that the energy required for the internal work of transpiration so

Table IX.—The Summarized Results of Table VIII, showing the Mode of disposal by the Leaf of the Energy flowing into it.

The Total Energy received = 100.

	Expt. I.	Expt. II.	Expt. III.	Expt. IV.	Expt. V.	Expt. VI.	Expt. VII.
<i>w.</i> Energy used for photosynthesis	0·42	1·59	1·66	1·32	0·49	1·34	1·16
<i>W.</i> „ transpiration...	9·67	53·60	57·01	35·64	52·72	15·64	16·42
<i>W + w.</i> Total energy expended in internal work	10·09	55·19	58·67	36·96	53·21	16·98	17·58
<i>R - Ra.</i> Solar radiant energy lost by transmission through leaf	35·31	35·30	35·32	35·28	35·30	30·00	30·00
<i>r.</i> Energy lost by re-radiation and air-convection	54·60	9·51	6·01	27·76	11·49	53·02	52·42
	100·00	100·00	100·00	100·00	100·00	100·00	100·00
	Expt. VIII.	Expt. IX.	Expt. X.	Expt. XI.	Expt. XII.	Expt. XIII.	
<i>w.</i> Energy used for photosynthesis	0·78	1·16	1·28	1·14	0·66	0·27	
<i>W.</i> „ transpiration...	10·21	18·47	60·03	35·60	48·39	53·30	
<i>W + w.</i> Total energy expended in internal work	10·99	19·63	61·31	36·74	49·05	53·57	
<i>R - Ra.</i> Solar radiant energy lost by transmission through leaf	30·03	27·20	27·24	27·20	31·40	31·40	
<i>r.</i> Energy lost by re-radiation and air-convection	58·98	53·17	11·45	36·06	19·55	15·03	
	100·00	100·00	100·00	100·00	100·00	100·00	

far exceeded the reception and absorption of solar energy, that the temperature of the leaf was lower than the surrounding air; in other words, the leaf was receiving energy from its surroundings in addition to that of the solar radiation incident upon it.

Owing to the desirability in these last-mentioned experiments of employing solar radiation of considerable intensity, direct control-experiments on assimilation could not be carried out simultaneously as they were in the previous experiments of Tables VIII and IX, where the insolation had been purposely lowered in intensity by suitable screening.

A close estimate of the rate of assimilation could, however, be arrived at from previous experiments, and the error introduced into the thermal results by this cause must be very small.

Table X.—Second Series of Experiments on the Thermal Interchanges between  
by *Revolving Sectors* Arranged to Cut Off a

No. of experiment and date.	Species of plant and general conditions of experiment.	Meteorological data.							Difference of temperature between leaf and air, °C.
		Percentage of sunshine recorded.	Dry bulb thermometer.	Wet bulb thermometer.	Partial pressure of water-vapour in air in millimetres of mercury.	Degree of humidity of air. Saturated air = 100.	Velocity of wind in kilometres per hour.		
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	
XIV. July 8, 1901	<i>Helianthus annuus</i> — Leaf A received full insolation, whilst B received exactly <i>one-half</i> of that incident on A	(A) 90 (B) 90	21·2 21·2	15·4 15·4	9·81 9·81	52 52	14·4 14·4	—0·17 —0·91	
XV. July 9, 1901	<i>Helianthus annuus</i> — Leaf A in full sunlight ..... Leaf B behind radial sectors arranged to cut off <i>one-half</i> of full radiation	(A) 100 (B) 100	22·2 22·2	15·1 15·1	9·13 9·13	46 46	8·0 8·0	—1·15 —1·46	
XVI. July 11, 1901	<i>Helianthus annuus</i> — Leaf A in full sunlight ..... Leaf B received <i>one-half</i> of solar radiation falling on A	(A) 100 (B) 100	27·2 27·2	19·0 19·0	11·5 11·5	43 43	12·0 12·0	—0·40 —1·84	
XVII. July 15, 1901	<i>Helianthus annuus</i> — Leaf A received full insolation Leaf B received three-fourths of full insolation	(A) 70 (B) 70	22·2 22·2	15·6 15·6	9·60 9·60	48 48	17·1 17·1	—0·74 —0·97	
XVIII. July 17, 1901	<i>Helianthus annuus</i> — Leaf A received full sunshine... Leaf B received three-fourths full sunshine	(A) 76 (B) 76	25·4 25·4	19·0 19·0	12·28 12·28	51 51	11·2 11·2	—0·82 —1·53	
XIX. July 18, 1901	<i>Helianthus annuus</i> — Leaf A received full sunshine... Leaf B received seven-eighths full sunshine	(A) 100 (B) 100	27·5 27·5	19·7 19·7	12·26 12·26	45 45	18·2 18·2	—1·45 —1·55	
XX. July 19, 1901	<i>Helianthus annuus</i> — Leaf A received full sunshine... Leaf B received seven-eighths full sunshine	(A) 75 (B) 75	27·6 27·6	19·6 19·6	12·03 12·03	43 43	11·7 11·7	—0·61 —0·84	

Leaves and their Surroundings, the Incident Solar Radiation being Graduated  
Definite Amount of the Incident Radiation.

Estimated temperature of leaf.		Excess of partial pressure of water-vapour in leaf over that of air in millimetres of mercury.	Assimilation in cubic centimetres of CO <sub>2</sub> per square decimetre per hour.	Transpiration in grammes of water per square decimetre per hour.	Loss or gain of energy by the leaf in calories per square centimetre of leaf-lamina per minute.							
(10)	(11)				(12)	(13)	R. Solar radiation incident on leaf.	a. Coefficient of absorption.	Ra. Solar radiation absorbed by leaf.	w. Energy expended in assimilation.	W. Energy expended in transpiration.	W + w. Total energy used for internal work.
	°											
21.0	8.65	*3.80	3.326	0.4547	0.686	0.3119	0.0031	0.3282	0.3313	—	0.0194	
20.3	7.87	*3.80	2.580	0.2273	0.686	0.1559	0.0031	0.2548	0.2579	—	0.1020	
21.0	9.33	*4.00	3.476	0.4798	0.686	0.3291	0.0033	0.3431	0.3464	—	0.0862	
20.7	8.99	*4.00	2.740	0.2399	0.686	0.1645	0.0033	0.2704	0.2735	—	0.1090	
26.8	14.66	*4.00	4.178	0.5492	0.686	0.3768	0.0033	0.4124	0.4157	—	0.0389	
25.3	12.44	*4.00	3.715	0.2746	0.686	0.1884	0.0033	0.3668	0.3701	—	0.1817	
21.4	9.32	*4.00	3.661	0.3931	0.686	0.2697	0.0033	0.3614	0.3647	—	0.0950	
21.2	9.09	*4.00	3.270	0.2948	0.686	0.2022	0.0033	0.3229	0.3262	—	0.1240	
24.6	10.68	*4.00	4.206	0.4993	0.686	0.3425	0.0033	0.4154	0.4187	—	0.0762	
23.8	9.60	*4.00	4.014	0.3744	0.686	0.2569	0.0033	0.3964	0.3997	—	0.1428	
26.0	12.69	*4.00	5.780	0.5504	0.686	0.3775	0.0033	0.5706	0.5739	—	0.1964	
25.9	12.54	*4.00	5.438	0.4806	0.686	0.3298	0.0033	0.5368	0.5401	—	0.2103	
27.0	14.44	*4.00	4.277	0.5337	0.686	0.3661	0.0033	0.4219	0.4252	—	0.0591	
26.7	13.97	*4.00	4.040	0.4666	0.686	0.3201	0.0033	0.3981	0.4014	—	0.0813	

Table X—

No. of experiment and date.	Species of plant and general conditions of experiment.	Meteorological data.						Difference of temperature between leaf and air, °C.
		Percentage of sunshine recorded.	Dry bulb thermometer.	Wet bulb thermometer.	Partial pressure of water-vapour in air in millimetres of mercury.	Degree of humidity of air. Saturated air = 100.	Velocity of wind in kilometres per hour.	
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
XXI. July 24, 1901	<i>Helianthus annuus</i> — Leaf A received full solar radiation Leaf B received five-eighths full solar radiation	(A) 13 (B) 13	17·4 17·4	16·2 16·2	12·89 12·89	87 87	20·9 20·9	+0·25 +0·09
XXII. July 21, 1901	<i>Senecio grandifolius</i> — Leaf A full solar radiation..... Leaf B <i>one-half</i> full solar radiation	(A) 52 (B) 52	22·5 22·5	17·2 17·2	11·52 11·52	79 79	15·5 15·5	+0·96 -0·41
XXIII. June 24, 1901	<i>Senecio grandifolius</i> — Leaf A full solar radiation..... Leaf B <i>one-half</i> full solar radiation	(A) 66 (B) 66	18·3 18·3	11·4 11·4	6·89 6·89	44 44	18·9 18·9	+1·02 -0·02
XXIV. June 25, 1901	<i>Senecio grandifolius</i> — Leaf A full solar radiation..... Leaf B <i>one-half</i> full solar radiation	(A) 46 (B) 46	19·4 19·4	13·2 13·2	8·10 8·10	48 48	12·8 12·8	+0·40 -0·23

N.B.—In the case of experiments marked thus \* the



*continued.*

(10)	Estimated temperature of leaf.	(11)	Excess of partial pressure of water-vapour in leaf over that of air in millimetres of mercury.	(12)	Assimilation in cubic centimetres of CO <sub>2</sub> per square decimetre per hour.	(13)	Transpiration in grammes of water per square decimetre per hour.	Loss or gain of energy by the leaf in calories per square centimetre of leaf-lamina per minute.							
(14)	R. Solar radiation incident on leaf.	(15)	a. Coefficient of absorption.	(16)	Ra. Solar radiation absorbed by leaf.	(17)	w. Energy expended in assimilation.	(18)	W. Energy expended in transpiration.	(19)	W + w. Total energy used for internal work.	(20)	r. Energy lost by re-radiation and air-convection.	(21)	(W + w) - Ra. Energy received from surroundings.
17.6	°	2.06	*4.00	0.4096	0.1179	0.686	0.0808	0.0033	0.0404	0.0437	0.0371	—			
17.5		1.96	*4.00	0.3303	0.0736	0.686	0.0505	0.0033	0.0333	0.0363	0.0139	—			
23.5		9.97	*4.00	2.179	0.4288	0.774	0.3319	0.0033	0.2151	0.2184	0.1135	—			
22.1		8.23	*4.00	1.763	0.2144	0.774	0.1659	0.0033	0.1736	0.1769	—	0.0485			
19.3		9.73	*4.00	1.744	0.4080	0.774	0.3158	0.0033	0.1718	0.1751	0.1407	—			
18.2		8.63	*4.00	1.599	0.2040	0.774	0.1579	0.0033	0.1576	0.1609	—	0.0030			
19.8		9.05	*4.00	1.470	0.2468	0.774	0.1910	0.0033	0.1463	0.1496	0.0414	—			
19.1		8.32	*4.00	1.183	0.1234	0.774	0.0955	0.0033	0.1167	0.1200	—	0.0245			

values were estimated, not obtained by direct experiment.



Table XI—*continued.*

	Expt. XX		Expt. XXI.		Expt. XXII.		Expt. XXIII.		Expt. XXIV.	
	A. Full inso-lation.	B. seven-eighths inso-lation.	A. Full inso-lation.	B. Five-eighths inso-lation.	A. Full inso-lation.	B. Half inso-lation.	A. Full inso-lation.	B. Half inso-lation.	A. Fully inso-lated.	B. Half inso-lated.
<i>w.</i> Energy used for photosynthesis	0.55	0.60	2.79	4.48	0.76	1.46	0.80	1.59	1.33	2.23
<i>W.</i> " " transpiration....	71.17	72.66	34.26	45.24	50.16	77.01	42.10	76.13	59.29	78.90
<i>W + w.</i> Total energy expended in internal work	71.72	73.26	37.05	49.72	50.92	78.47	42.90	77.72	60.62	81.13
<i>R - Ra.</i> Solar radiant energy lost by transmission through leaf	28.28	26.74	31.40	31.38	22.59	21.53	22.59	22.28	22.60	18.84
<i>r.</i> Energy lost by re-radiation and air-convection	—	—	31.55	18.90	26.49	—	34.51	—	16.78	—
	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

*Jodrell Laboratory,  
Royal Gardens, Kew.*